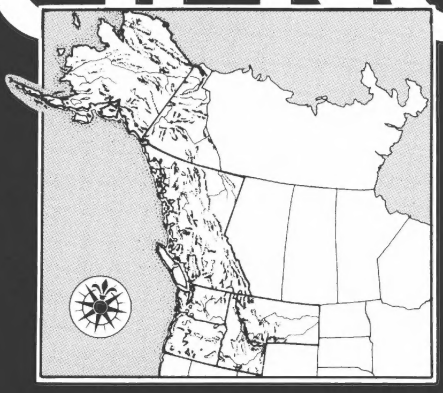
February 1992 Volume 66, Number 1

OIL SPILL—A YEAR LATER

NORTHWEST SCIENCE



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(Founded 1923)

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Northwest Science Meeting—March 24-28, 1992: A Preview of Coming Attractions

The **Northwest Scientific Association,** the **American Fisheries Society,** the **Society for Northwestern Vertebrate Biology,** and the **Lichen Guild** will meet jointly in Bellingham, Washington, March 24-28. The general theme of the meeting will be **biodiversity.** Some major activities of the meeting include the following:

Symposia

Biodiversity (Wednesday 25 March, topics listed alphabetically by author):

- "Economics of biodiversity: non-market values" (Daniel Hagen)
- "Preserving biodiversity at the landscape level" (Peter Haug)
- "Biological diversity and forest management: a look to the future" (Ross Kiester)
- "Status and importance of stocks in the Pacific salmon resource" (Jim Lichatowich)
- "Biodiversity at risk: saving all the pieces" (Elliot Marks)
- "Landscape management in a changing environment" (David Peterson)
- "A National Park Service perspective on biological diversity" (Ed Schreiner)
- "Department of Natural Resources strategy for biodiversity management" (John Shumuay)
- "Economics of biodiversity: market values" (James Vincent)

Wetlands: Useful tools to assess wetlands functions (Friday 27 March)

Participants include: Ellis Clairain (US Corps of Engineers), Charles Simensted (University of Washington), Ron Thom (Battelle Marine Science Labs), Gary Williams (Environmental Consultant), and Joy Zedler (San Diego State University).

Seminar (Wednesday evening)

"Understanding nature through art" by Tony Angell

General Topics Sessions

Society for Northwestern Vertebrate Biology:

(1) "Biology and management of northwestern vertebrates"
(2) "Taxonomy, distribution, and status of amphibians, reptiles, mammals and birds in the Northwest"

Joint sessions (contributed papers) (Thur. and Fri.)

- Aquatic ecology
- Botany
- Forestry
- Geology/geography
- Lichens & mosses
- Marine biology
- Zoology

Lichen Workshop (Friday)

Field Trips (Saturday 28 March)

- Skagit River—wetlands
- Noisy Creek—old growth forest
- Washington Park—spring wildflowers and lichens
- San Juan Islands—marine biology

For further information, registration forms, etc., contact: Ron Taylor, Biology Department, Western Washington University, Bellingham, Washington 98225.

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Fate of Bunker C Fuel Oil in Washington Coastal Habitats Following the December 1988 *NESTUCCA* Oil Spill

Abstract

Following the December 1988-spill of 230,000 gallons of Bunker C fuel oil from the barge *NESTUCCA*, a year-long monitoring program was conducted to follow the fate of spilled oil in selected intertidal and shallow subtidal habitats of the Washington coast, including a 40-mile-long strip of Olympic National Park (ONP). Following clean-up, beach surveys were conducted in July and September 1989 and February 1990 at eight coastal sites inside ONP: four oiled areas, four unoiled areas; and at four oiled sites (coastal and estuarine) outside ONP. The finding of only trace levels (63-250 μg/g dry weight by infrared spectrometry) of oil in surface (0-15 cm in depth) sediments associated with coastal sites 13 months after oiling suggested that depuration had occurred rapidly and that little oil residual remained. The essentially background levels (mostly <45 ng/g dry weight by gas chromatographic mass spectrometry) of aromatic hydrocarbons found in invertebrates associated with oiled sediments also suggested that most oil had been rapidly metabolized and depurated or was no longer biologically available. Factors contributing to these findings likely included: 1) the time of year when the spill occurred, 2) the type of beach or coastline affected, and 3) the timely and efficient clean-up. Most spilled oil congealed before stranding due to cold air and water temperatures. The area of the coast most affected consisted of unprotected, high-energy, sand beaches and rocky headlands, which self-cleanse rapidly. Finally, clean-up was immediate and congealed oil was easily removed from affected beaches.

Introduction

On December 23, 1988, the barge *NESTUCCA* was accidently struck by its tow, a Souse Brothers Towing tug, releasing approximately 230,000 gallons of Bunker C fuel oil and fouling beaches from Grays Harbor, Washington, north to Vancouver Island, British Columbia. Affected beaches in Washington included a 40-mile-long strip that recently had been added to Olympic National Park (ONP).

Following the spill, the efficacy of clean-up, the extent of weathering and the release of persistent hydrocarbons to the water column from oil buried both intertidally and subtidally along ONP beaches were largely unknown. Past experience indicated that buried oil from the spill could remain unweathered for several years or more (Teal *et al.* 1978, Burns and Teal 1979). The potential for long-term effects of the *NESTUCCA* barge spill on marine life suggested that a monitoring program should be initiated to assess fate and effects of unrecovered oil on the ONP beaches.

This paper presents the results of a year-long monitoring program to follow the fate of spilled oil on selected ONP beaches and on other Washington coast habitats. The key questions addressed by this research included: 1) How much oil remained on Washington beaches following clean-up and weathering; 2) To what extent were intertidal and shallow subtidal biotic assemblages contaminated; and 3) How rapidly did oil leave the system? Factors likely influencing weathering and depuration of hydrocarbon burdens from affected ecosystem components are also discussed.

Methods

Study Sites

Preliminary to sampling design, study sites were selected by consensus of staff from ONP, the Minerals Management Service (MMS), and Battelle, Marine Sciences Laboratory (MSL). First-hand information on the distribution and density of oil and the implementation of clean-up procedures was provided by ONP. Additional information on shoreline contamination (distribution and density of oil) was obtained from the Washington State Department of Ecology (Holcomb 1989).

Eight sites were selected from inside the Park; four from areas with moderate or heavy contamination (if possible), and four from no known or very light contamination, to serve as reference sites (Table 1). Additionally, four study sites with moderate or heavy contamination were selected from outside the Park. Site selection criteria included the

TABLE 1. Study sites selected to follow the fate of Bunker C fuel oil spilled on Washington coastal beaches in December 1988.

Beach	Location	Status	Substrate
Wedding Rocks	Olympic National Park	Light Oil	Rock/Cobble
Norwegian Memorial North	Olympic National Park	Heavy Oil	Rock/Cobble
Norwegian Memorial South	Olympic National Park	Reference	Rock/Cobble
Kayostla Beach North	Olympic National Park	Moderate/ Heavy Oil	Rock/Cobble
Cedar Creek	Olympic National Park	Reference	Sand/Cobble
Hole-in-the-Wall	Olympic National Park	Reference	Rock/Cobble
Second Beach	Olympic National Park	Moderate/ Heavy Oil	Sand
Ruby Beach	Olympic National Park	Reference	Sand
Whale Creek	Quinault Indian Res.	Moderate Oil	Sand
Pt. Grenville	Quinault Indian Res.	Light Oil	Sand
Ocean Shores-North Jetty	Grays Harbor	Heavy Oil	Sand
Sand Island	Grays Harbor	Heavy Oil	Sand

extent of oiling, the presence of valued biological communities, beach substrate type (sand, gravel, cobble, rock), and accessibility. Although it was particularly important to sample cobble beaches (such areas do not naturally depurate rapidly), only one beach in ONP (Norwegian Memorial North) having relatively deep deposits (>15 cm) of gravel and cobble was also heavily oiled (Holcomb 1989). This was the only site found by clean-up crews and staff from ONP to contain buried oil. On the other cobble beaches sampled, the depth of cobble and gravel was generally <15 cm and was typically underlaid with bedrock.

All oiled beaches in this study were cleaned within the first month following the spill. At a minimum, cleaning involved the removal or burning of oil-spattered logs. Maximum cleaning included the collection of oil using pom-poms and absorbent pads and the removal of oil mats and oiled debris. All beaches along the Washington coast may have received some oiling, if not from the December 1988 spill, then from indiscriminate bilge pumping and from small, unreported oil spills from coastal shipping in the past.

Figure 1 shows the locations of study sites and also the locations of known natural oil seeps. Natural oil and gas seeps occur near the Pysht River, at Hoh Head near Ruby Beach, at Shi Shi Beach, east along the Hoh River (not shown) and near Taholah on the Quinault River (Snavely and Kvenvolden 1989). The oil seep at Ruby Beach is the closest to any of our sampling sites but is still 2 km distant. It is not likely, then, that oil released from this seep, or other seeps, confounded sampling and subsequent chemical analyses at any of the designated study sites. Also, because of the patchy nature of the oiling of ONP beaches, the relatively close location of oiled and reference sites (Norwegian Memorial North and South and Kayostla Beach North) was not considered a problem.

Selection of Survey Dates

Beach surveys were scheduled during the lowest tides in July and September 1989 and in February 1990. The July and September surveys were to occur when beach accretion was at or near maximum annual height. The February survey was to coincide when beach accretion was minimal, i.e., when target beaches were near their lowest height.

Sediment Sampling

As shown in Figure 2, sediments at each of the 12 study sites were sampled at the +8.2-ft (+2.5-m), +1.1-ft (+0.5-m), −1.7-ft (−0.5-m), and −3.0-ft (−1.0-m) tidal contours along single, randomly located transects placed perpendicular to the coastline.

At the designated sampling locations, a 0.5-L sediment sample from a 0.1-m^2 area was collected from the top 15 cm of the beach surface. Sediments from cobble areas were necessarily collected from depths shallower or deeper than 15 cm, depending on the depth of the cobble or the presence of bedrock. In many cases sediments from the rock/cobble beaches were collected from sediment pockets among and under small boulders and rocks. Sediment samples were taken from the beach using a solvent-rinsed stainless-steel coring device and placed in labeled and dated sampling jars, also solvent-rinsed. Sediment composition was also recorded. To attest to the cleanliness of sampling equipment, a control (blank) sample was

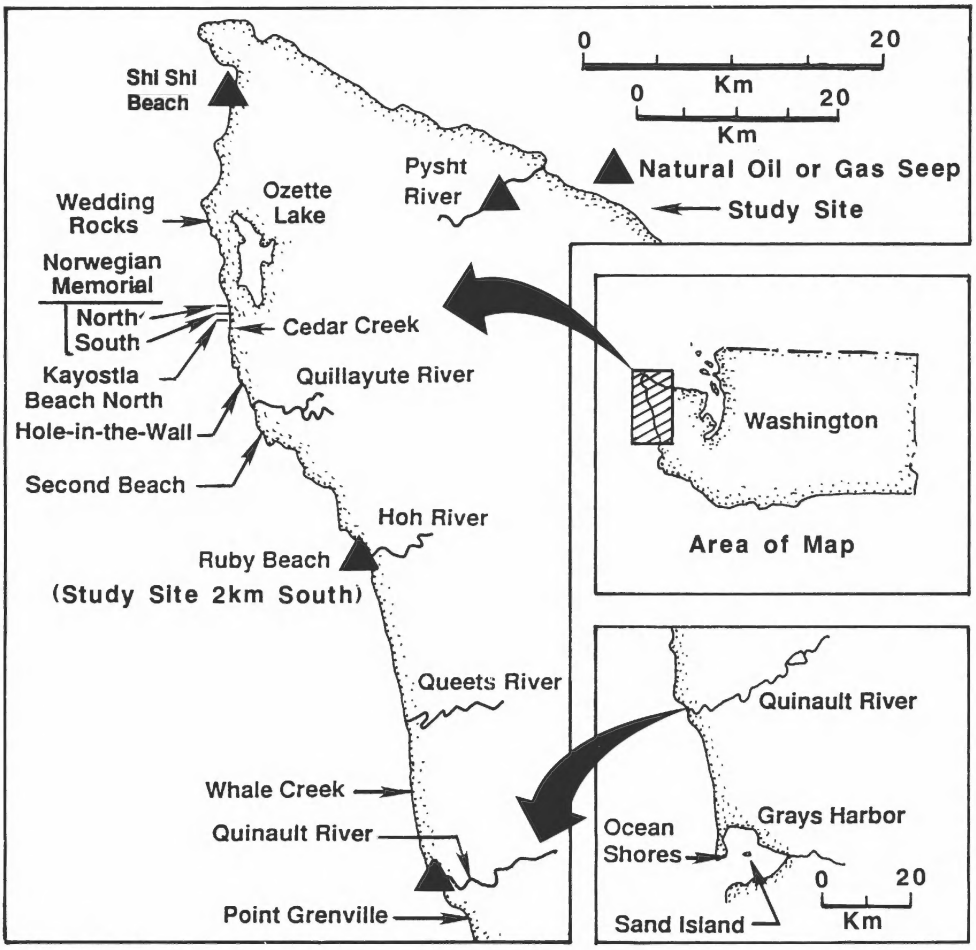

Figure 1. Relative locations of each sutdy site and known naturally occurring oil and gas seeps along the Washington Coast.

collected once each day. The sampling jar used for this purpose was handled in the same way as all other sampling jars except that no sediment was placed in the sampling jar. Upon return to the laboratory, the control (blank) sample jar was extracted in the same way as those jars containing sediments. Target sampling requirements for intertidal and shallow subtidal sediments are summarized in Table 2.

For the first survey, elevations (tidal height) at the four positions along the transect line were determined by level and stadia rod referencing known tidal heights. Distances to each sampling location on each transect also were recorded, and a monument was placed at the high-tide-line of each transect. During the second and third surveys, sampling locations on each transect were determined solely by distance from the high-tide-line monument.

Compositing

Sediment samples were composited to reduce costs of chemical analyses and to maintain large spatial coverage. Each sample was homogenized by mixing in a stainless steel bowl until uniformly colored and split in half. One-half was composited with the

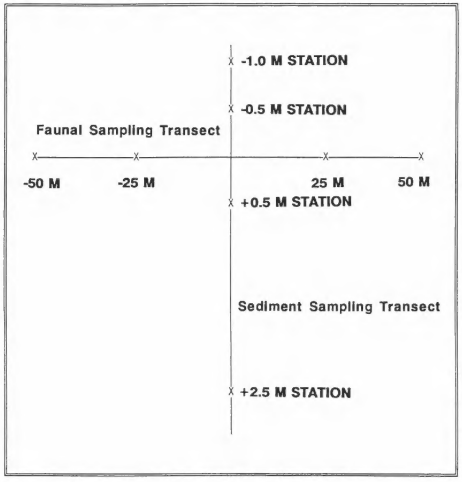

Figure 2. Sediment and faunal sampling stations (X) form perpendicular transects such that each sampling station lies within a specific tide-height contour. Sediment sampling stations are spaced logarithmically within intertidal and subtidal sampling zones while the faunal sampling stations are equally spaced away from the sediment sampling transect between the +0.5 m and −0.1 m tide-height contour.

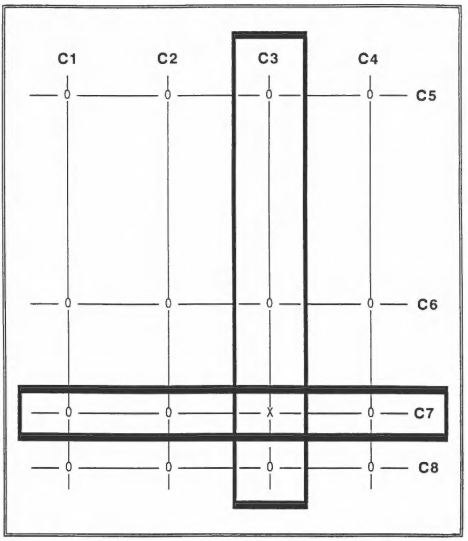

Figure 3. Compositing design for which samples are composited across columns (C1 to C4) and Rows (C5 to C8). This design preserves the location of contamination without requiring chemical analysis at every sampling station (0). In this scenario, high oil residue was detected in composites C3 and C7, indicating contamination at sampling-station X.

remaining samples from the same transect; the other half was composited with samples from the same tidal contour from transects with the same designation of contamination (oiled or unoiled). Compositing samples from similar columns (transects) and rows (tidal contours) of a lattice design preserves information on the location of oil residue without requiring chemical analysis for each sampling station. As shown in Figure 3, compositing samples from transect C3, and from tidal contour C8 located contamination at sampling station X.

Samples composited in this way were not diluted with clean sediments below a selected level of concern (LC) so that information on the location of potential oil was not lost. Compositing was done with equal quantities of materials from each sampling location included in the composite so that the analytical results represented the mean concentration of oil residue for each location sampled. To minimize dilution, the maximum number (N) of samples that should be composited was determined by the formula

$$N = LC/DL$$

where DL is the analytical detection limit (Skalski and Thomas 1984). Data from Vanderhorst et al. (1980) showed that along the Strait of Juan de Fuca, background levels of total hydrocarbon concentrations ranged form 20 to 140 $\mu g/g$ in

TABLE 2. Target Sampling Requirements of Intertidal and Shallow Subtidal Habitats for Each Survey

Sample Type	No. Samples/ Station	No. Stations/ Transect	No. Transects	Total Samples	Composites Analyzed (a)
Sediment (IR)	1	4	12	48	26
Sediment (GC)	1	4	12	48	16
Tissue (GC)	1	4	12	48	26

(a) Includes duplicates.

intertidal sediments. Based on this data, the LC of 100 μg/G was selected for the present study. The DL of infrared spectrophotometry (IR) for total hydrocarbon concentration is about 20 μg/g; thus, to minimize dilution, no more than five samples were composited. For gas chromatography (GC), the DL for both polycyclic aromatic and saturate hydrocarbons in sediments was about 10 ng/g, yielding an N much greater than that for IR.

Faunal Sampling

Faunal samples were collected from four sampling stations along a 100-m transect established parallel to the coastline along a tidal-height contour between the +1.1-ft and −3.0-ft sediment sampling stations (Figure 2). These four sampling locations were placed 25 and 50 m either side of the sediment sampling transect.

If a sandy beach was selected for sampling, razor clams (*Siliqua patula*) were collected. From a rock/cobble beach, California mussels (*Mytilus californianus*) were sampled. If this species was unavailable, organisms of opportunity (polychaetes, limpets, snails, chitons, crustaceans) were collected. The organisms were wrapped in ashed aluminum foil, placed on ice, and transported to the laboratory within 48 hours of collection, where they were immediately frozen at −18°C until dissection. After freezing, samples of tissue were obtained through dissection and packed in wide-mouth glass jars with Teflon™-lined screw caps. These samples were refrozen and stored at −75°C until analysis. Target sampling requirements for tissues are summarized in Table 2.

Compositing

Tissue from 3 to 5 clams, 4 to 12 mussels, or enough organisms of opportunity to produce a minimum of 10 g wet weight, from each of the two stations equally distant from the sediment sampling transect, were combined for a composite chemical analysis.

Sampling Exceptions

Because of severe weather conditions, high wave action, and periodic unavailability of appropriate organisms, it was not always possible to collect a full complement of sediment and faunal samples at each study site. Of 12 target sediment samples per study site (four from each survey), all sites had a minimum of 8 target samples collected, except Sand Island which had three target samples collected. Sand Island was surveyed only twice (September 1989, March 1990). All target sediment composites were made, again with the exception of Sand Island from the first survey. Of a target six faunal samples per sampling site (two from each survey), six sites had all six samples collected, again except for Sand Island where no faunal samples were collected. The intertidal fauna at Sand Island appeared to be limited to sparse populations of clams occupying sediments too dense to excavate using a clam gun.

When possible, extra sediments, cores, and/or faunal samples were collected at some of the sampling sites during each of the surveys. Because of suspected contamination from a small, yet unreported oil spill occurring off the Washington coast in February 1990, extra samples were collected and analyzed from Hole-in-the-Wall and Ruby Beach, both reference sites, during the third survey. Two sediment samples were collected and analyzed from a site further north of the Norwegian Memorial (designated as HNMX), and from Goose Island in Grays Harbor during the third survey. The HNMX site is the location of intertidal community studies conducted by the University of Washington. Because of the very gradual beach slope at Sand Island, sediment samples were collected at +15.2-, +13.3-, +8.2-, and +7.8-ft tidal levels. The +7.8-ft sample was composited as if it were the +1.1-ft sample.

Analytical Chemistry

Sediments

Chemical analysis for sediments was conducted in stages. Composite samples first were screened for oil by analyzing for total oil and grease using infrared spectrophotometry (IR), a relatively inexpensive method of analysis. Samples were analyzed by a Beckman Acculab™ Model 4 Infrared Spectrophotometer within a spectral range of 3200 to 2600 cm-1 and a scan time of 25 to 27 min. Sediment was extracted within freon following Standard Method 503 (American Public Health Association 1985). To distinguish between the target oil and

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oils of biogenic origin, the extract was mixed with silica gel to remove fatty acids.

Sediment samples showing a signal above detection were analyzed by GC for a more accurate characterization of the source of contamination (finger-printing). Samples were analyzed using a Hewlett Packard (HP) 589AO GC equipped with a HP 7673A automatic sampler and a flame ionization detector (FID) or a 5970 mass-selective detector (MS). An HP 5895A gas-chromatographic workstation was used for control of the GC, integration, quantification, and preparation of the chromatograms. Sediment samples including control blanks were extracted using a process developed by Krahn *et al.* (1988).

Tissues

Composite tissue samples (enough to produce a minimum of 10 g wet weight) from each site, were homogenized using a Tekmar Tissumizer™. Five gram subsamples of wet tissue were digested with 30 ml of 6 M KOH at 35°C for 18 hours, then extracted three times with 30 ml of ethyl ether, followed by alumina column clean-up to remove matrix interferences (U.S. Environmental Protection Agency 1986). As with sediment samples, tissue samples were analyzed using the HP 5890A GC equipped with an HP 7673A automatic sampler and an FID, or an HP 5970 MS. The HP 5895A gas-chromatographic workstation controlled the GC and was used to prepare the chromatograms.

For both tissues and sediments, petroleum residues were characterized by relative peak areas for the concentration of individual identified normal branched saturate and polycyclic aromatic hydrocarbons, the ratios of nC_{17}/Pristane and nC_{18}/Phytane, and the carbon preference index (CPI), i.e., (odd to even saturate ratio). Changes in one or more of these characteristics provided an estimate of weathering and/or the degree of mixing with other potential sources of hydrocarbons. Chromatograms from all sediment and tissue samples were compared with chromatograms from identical analyses of the spilled oil obtained from the Washington State Department of Ecology.

All analytical and associated quality-assurance and -control procedures (including the use of standard reference materials, chemical spikes, and duplicate analyses) followed *Recommended Protocols for Measuring Selected Environmental Variables in Puget Sound* (Tetra Tech, Inc. 1986).

Results and Discussion

Sediments

Total Oil and Grease

Those analytical results showing above detection limits are presented in Table 3. Because all composites collected during the first survey (July 1989) contained essentially background levels (<50 μg/g dry weight) of total oil and grease, these composites were not analyzed further.

From the second survey (September 1989), only the extra sediments from Sand Island contained detectable levels of oil and grease, with concentrations of 6,255 and 19,015 μg/g dry weight in the sediments from the +15.2- and +13.3-ft tidal levels, respectively. Oily residue was clearly visible in these samples, and a strong petroleum (Bunker C) odor was evident. These sediments were further analyzed for aromatic and saturate hydrocarbons. Because levels of total oil and grease at Norwegian Memorial, Kayostla Beach, and Whale Creek were below detection, extra cores collected from these sites were not analyzed.

Detectable levels of total oil and grease were found in several sediment composites and extra sediments from the third survey (February 1990), including samples from Wedding Rocks, Norwegian Memorial North, Kayostla Beach and Hole-in-the-Wall. The Oiled Park Beaches composite, which included sediments from the −3.0-ft tidal contour at Wedding Rocks, Norwegian Memorial North, and Kayostla Beach North, suggested that this elevation contour was potentially contaminated with oil. These eight composites, along with suspect extra sediments, were further analyzed for aromatic and saturate hydrocarbons.

Aromatic and Saturate Hydrocarbons

Sediment concentrations of aromatic hydrocarbons are presented in Table 4. The sample from Wedding Rocks revealed moderately low concentrations (2,875 and 18,236 ng/g dry weight, respectively) of both aromatic and saturate hydrocarbons. The extra sediment from Norwegian Memorial (+82) also contained moderately low levels of both hydrocarbon fractions: 1553 ng/g of aromatics and 14,178 ng/g of saturates. Only the extra

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TABLE 3. Sediments from Washington coast beaches with above-detection levels of total oil and grease (μg/g dry weight) as detected by infrared spectrophotometry.

Composites (a)		
Location (Tidal Height in ft)	Survey Date	Oil and Grease (μg/g)
Wedding Rocks	Feb/Mar 1990	63
Norwegian Memorial North	Feb/Mar 1990	72
Kayostla Beach North	Feb/Mar 1990	154
Oiled Park Beaches (−3.0) (b)	Feb/Mar 1990	251
Extra Sediments		
Location (Tidal Height in ft)	Survey Date	Oil and Grease (μg/g)
Sand Island (+13.2)	Sept 1989	19015
Sand Island (+15.2)	Sept 1989	6255
Norwegian Memorial (+8.2)	Feb/Mar 1990	115
Norwegian Memorial (+1.1)	Feb/Mar 1990	73
Hole-in-the-Wall (+15.0)	Feb/Mar 1990	170
Ruby Beach (+14.0)	Feb/Mar 1990	86

(a) Composite of all four samples collected from each transect.

(b) Composite of −3.0 ft samples from Wedding Rocks, Norwegian Memorial North, Kayostla Beach North, Second Beach.

TABLE 4. Sediment concentrations of total aromatic (PAH) and saturate (C_9-C_{36}) hydrocarbons (ng/g dry weight) detected by GC/FID and GC/MS.

Location (Tidal Height in ft)	Survey Date	Total PAH	Sum C9-C36
	Composites (a)		
Wedding Rocks	Sept 1989	2876	18236
Wedding Rocks	Feb/Mar 1990	478	2236
Norwegian Memorial North	Feb/Mar 1990	80	1792
Kayostla Beach North	Feb/Mar 1990	64	2158
Oiled Park Beaches (−3.0) (b)	Feb/Mar 1990	59	901
Cedar Creek	Feb/Mar 1990	164	2756
Sand Island	Sept 1989	(c)	455
	Extra Sediments		
Sand Island (+13.2)	Sept 1989	27624	1570069
Sand Island (+15.3)	Sept 1989	83399	488977
Norwegian Memorial (+8.2)	Feb/Mar 1990	1268	8893
		1553 (d)	14178 (d)
Hole-in-the-Wall (+15.0)	Feb/Mar 1990	80	3829
Ruby Beach (+14.0)	Feb/Mar 1990	45	2354
Ocean Shores (+11.0)	Sept 1989	(c)	748

(a) Composite of all four samples collected from each transect.

(b) Composite of −3.0 ft samples from Wedding Rocks, Norwegian Memorial North, Kayostla Beach North and Second Beach.

(c) Not Detected; detection limits were 3 to 10 ng/g for individual aromatic hydrocarbon compounds, and 100 ng/g for individual saturate hydrocarbon compounds.

(d) Duplicate analysis.

sediments from Sand Island showed relatively high concentrations of both categories of hydrocarbons. The sums of the aromatic hydrocarbons for these samples were 27,624 and 83,399 ng/g dry weight, respectively. The sums of the resolved saturate hydrocarbons for these samples were 488,977 and 1,570,069 ng/g, respectively. The extra Ocean Shores sample and the composite from Sand Island demonstrated less than detectable concentrations (<10 ng/g dry weight) of individual aromatic hydrocarbons, and very low levels (748 and 455 ng/g dry weight, respectively) of individual saturate hydrocarbons. The Cedar Creek composite was used for quality assurance and contained 164 ng/g dry weight of aromatic hydrocarbons and 2756 ng/g dry weight of saturate hydrocarbons, both relatively low levels.

Invertebrate Tissues

Tissues from Norwegian Memorial North (+25 m) and Wedding Rocks (+25 m) contained from 90 to 100 ng/g dry weight total aromatic hydrocarbons (Table 5). All other tissue concentrations were below 50 ng/g, and most were less than 20 ng/g. The extra tissue sample collected from the University of Washington site north of Norwegian Memorial North indicated a total aromatic hydrocarbon concentration of 24 ng/g (data not shown).

Tissue samples from Whale Creek and Point Grenville had the highest concentrations of total resolved saturate hydrocarbons, 23,650 and 22,349 ng/g dry weight, respectively (Table 5). However, tissue samples from Kayostla Beach and

TABLE 5. Selected tissue concentrations of total aromatic (PAH) and saturate (C_9-C_{36}) hydrocarbons (ng/g dry weight).

Location (a)	Tissue (b)	Survey Date	Total PAH	Total C9-C36	Sum Even C10-C36
Wedding Rocks (+25)	CM	July/Aug 1989	43	7745	4293
	CM	Sept 1989	100	11945	1523
	CM	Feb/Mar 1990	29	2085	(d)
Norwegian Memorial North (+25)	CM	July/Aug 1989	95	10923	5592
	C,S	Sept 1989	44	5850	2198
	CM,L,C,S	Feb/Mar 1990	90	3166	990
Kayostla Beach North (+25)	CM,L	July/Aug 1989	22	5619	2739
	L,C,S	Sept 1989	23	13137	9831
	L,C,S	Feb/Mar 1990	(d)	2421	1225
Hole-in-the-Wall (+25)	CM,L	July/Aug 1989	15	7637	3879
	CM,L,C,S	Sept 1989	8	13478	8351
	CM	Feb/Mar 1990	20	3075	917
Cedar Creek (+25)	CM	July/Aug 1989	8	7896	4195
	CM,C,S	Sept 1989	(d)	7611	3145
	CM	Feb/Mar 1990	19	421	881
Whale Creek (+50)	RC, DC	July/Aug 1989	7	23650	3748
	MS,H	Sept 1989	(d)	(d)	(d)
	(c)	Feb/Mar 1990	–	–	–
Pt. Grenville (+25)	CM,RC	July/Aug 1989	(d)	4151	3611
	RC,MS	Sept 1989	21	22349	4384
	CM	Feb/Mar 1990	(d)	(d)	(d)
Ocean Shores (+50)	RC,CM	July/Aug 1989	(d)	2166	1377
	CM	Sept 1989	12	1046	536
	CM	Sept 1989	(d)	6583 (e)	3694 (e)

(a) Composite from each of two stations either side and equal distance (25 or 50 m) from sediment sampling transect.

(b) CM = California mussel; L = shield limpet; AC = assorted crustacea; S = snails; C = chitons; RC = razor clams; DC = Dungeness crabs; MS = mud shrimp; H = beach hoppers.

(c) No organisms sampled due to severe weather.

(d) Not detected; detection limits were 3 to 10 ng/g for individual aromatic hydrocarbon compounds, and 100 ng/g for individual saturate hydrocarbon compounds.

(e) Duplicate analysis.

Hole-in-the-Wall had the highest concentrations of even saturate hydrocarbons, 9831 and 8351 ng/g dry weight, respectively, which do not include those of biogenic origin.

Source Identification

Sediments

Chromatograms of oil (aromatics fraction) associated with Sand Island sediments in September 1989 display patterns strikingly similar to those of Bunker C collected from the barge *NESTUCCA* by the Washington State Department of Ecology in December 1988 (Figure 4). The lower CPI values (< 1) associated with the Sand Island sediment samples also are indicative of an anthropogenic source of contamination (Table 6). The CPI values for the *NESTUCCA* oil, Alaska North Slope (ANS) crude oil, and Sand Island sediments are all essentially the same (0.90-0.94).

TABLE 6. Ratios of nC_{17}/Pristane, nC_{18}/Phytane, and the Carbon Preference Index (CPI) of Reference Oils and Selected Sediment Samples

	nC_{17}/ Pristane	nC_{18}/ Phytane	CPI
Reference Oils			
NESTUCCA Oil	1.83	1.27	0.90
Alaska North Slope Crude Oil	1.54	1.78	0.94
Sediment Samples (Tidal Height in ft)			
Sand Island (+15.2)	1.33	0.90	0.94
Sand Island (+13.3)	1.67	1.16	0.92
Oiled Park Beaches Composite (−3.0) (a)	(b)	(b)	0.67
Hole-in-the-Wall (+15.0)	(b)	(b)	0.68
Ruby Beach (+14.0)	(b)	2.20	1.02
Norwegian Memorial Extra (+8.2)	0.34	1.33	1.11
Norwegian Memorial Extra (+1.1)	0.51	(b)	0.78

(a) Composite of −3.0 ft samples from Wedding Rocks, Norwegian Memorial North, Kayostla Beach North, Second Beach.

(b) Not calculated because target hydrocarbons not detected.

Additionally, relatively little change is observed in the ratios of nC_{17}/Pristane and nC_{18}/Phytane when the Sand Island samples are compared with

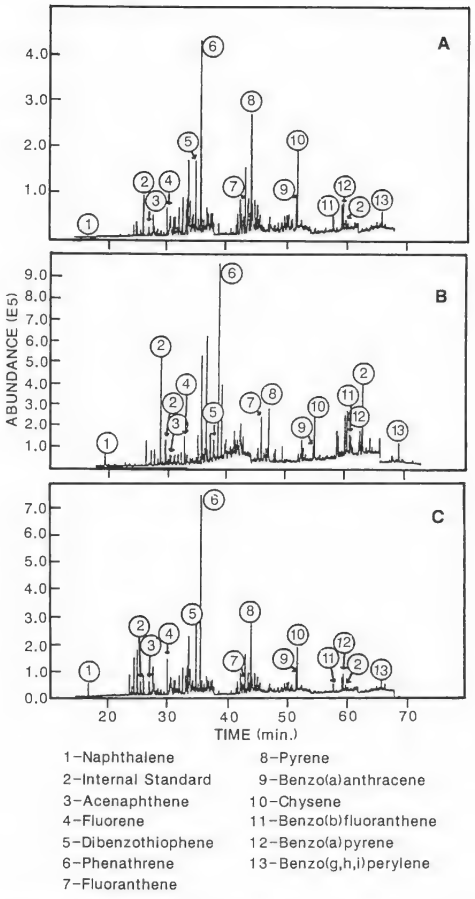

Figure 4. Total Ion Chromatograms (Polynuclear Aromatic Hydrocarbons) for Surface Sediments from Sand Island (A) and Norwegian Memorial-University of Washington Transect (B) Compared with the Total Ion Chromatogram for *NESTUCCA* Oil. (C) (The symbol E5 denotes values times 10^5.)

the *NESTUCCA* oil (Table 6). Significant changes have been reported in these ratios after six to nine months of weathering of intertidal sediments amended with ANS crude (Anderson *et al.* 1978), suggesting the presence of hydrocarbon degrading microorganisms (Blumer and Sass 1972). The finding of little change in these key hydrocarbon ratios indicates that biodegradation played a relatively minor role in the weathering of the Sand Island samples. This is not surprising, since the oil on Sand Island was buried just beneath the surface

(< 5 cm in depth) in relatively coarse sand in the high (+13.3 to +15.2-ft) intertidal zone.

The lack of significant weathering is also evident in the chromatograms of aromatic hydrocarbons from the Sand Island samples. The only significant changes that occurred are associated with the more volatile compounds. While concentrations of the more volatile compounds from the *NESTUCCA* oil are relatively low, the notable difference when comparing the aromatic hydrocarbon fraction of each chromatogram is the absence of napthalene from the Sand Island samples. There are, however, few other changes. Dibenzothiophene, phenanthrene, pyrene, chrysene, benzo(b)fluoranthene, and benzo(g,h,i,)perylene all persist in the Sand Island samples at generally the same relative concentrations as in the *NESTUCCA* oil.

While not shown, changes in saturate hydrocarbons were slight. As anticipated, some of the saturate hydrocarbons (C_9-C_{13}), although present in the *NESTUCCA* oil, were not detectable in either of the Sand Island samples. However, the remaining saturate hydrocarbons (C_{14}-C_{36}) were detected in the Sand Island samples, generally at the same relative concentrations as in the *NESTUCCA* oil.

Sediments collected during the third survey from the University of Washington study site north of Norwegian Memorial (Figure 4) and from Wedding Rocks, Norwegian Memorial North, Kayostla Beach North, and Second Beach (chromatograms not shown) may contain remnants of weathered Bunker C oil. The relative concentrations of fluorene, fluoranthene, pyrene, benzo(a)anthracene, chrysene, benzo(b)fluoranthene, benzo(a)pyrene, and benzo(g,h,i)perylene are comparable to the *NESTUCCA* oil. A complication to source identification, however, is that these samples contain other hydrocarbon components which are not consistent with Bunker C oil and may be of a biogenic origin.

Invertebrate Tissues

Chemical analyses of mussels, razor clams and other invertebrates revealed little information useful in determining the origin of essentially trace quantities of aromatic hydrocarbons contained in some of their tissues. While no naphthalenes were found in any of their tissues, phenanthrenes occurred in tissues from seven of twelve beaches sampled, including Ocean Shores, Point Grenville, Second Beach, Kayostla Beach, Norwegian Memorial North and South (including the transect sampled by the University of Washington), and Wedding Rocks. However, phenanthrene concentrations were generally less than 20 ng/g.

Perspective on Levels of Residual Oil Contamination

Although relatively high concentrations of oil (6,255 and 19,015 μg/g dry weight by IR) were found on Sand Island in Grays Harbor during the second survey, the relatively low concentrations of oil (63 to 250 μg/g by IR), essentially trace amounts, associated with the coastal stations during the third survey suggest that relatively little oil remains from the 1988 *NESTUCCA* spill. The relatively high concentrations of oil found on Sand Island were restricted to a narrow band 3 to 4 m wide over a 10- to 13-m stretch of beach on the southwest side of the Island. Attempts to relocate this band of oil during the third survey proved unsuccessful, further suggesting that weathering and depuration proceeded rapidly.

Interestingly, oil was not found associated with beaches hypothesized to be oiled (Kayostla, Norwegian Memorial, Wedding Rocks) until the third survey (February 1990). Low concentrations of oil were also detected at Ruby Beach and at Hole-in-the-Wall (both hypothesized unoiled beaches), although analyses of all samples collected from both beaches during the first and second surveys (July and September 1989, respectively) failed to detect the contaminant. While it is difficult to totally eliminate the possibility of altogether missing the oil on our first two surveys of oiled beaches, a possible explanation for not detecting oil on sand beaches is associated with the normal cycle of beach accretion and erosions. Because the spill occurred in December and January, when beaches were fully eroded, it follows that as beaches accreted sediments during summer and autumn months (also at the time of our first and second surveys), oil not removed by the clean-up crews potentially could have been buried and hence inaccessible to our sampling. We generally sampled to a depth of 15 cm, while beach accretion may total 1 to 2 m. Hence, when the beaches again eroded in the winter of 1990 (at the time of our third survey), the potentially buried oil could have again become accessible to our sampling methods. This explanation, however, might not equally apply to rocky beaches.

The finding of essentially little more than background concentrations of total oil and grease during the third survey (13 months after the spill) also suggested that weathering and depuration occurred more rapidly than indicated by the available and relevant literature. For comparisons, Bunker C fuel oil spilled from the *ARROW* in Chedabucto Bay, Nova Scotia in February 1970, was much more persistent (Vandermeulen and Gordon 1976, Vandermeulen *et al.* 1977). Seven years after the spill, analyses of subsurface sediments (7 to 11 cm in depth) collected from the mid-tide level revealed concentrations of hydrocarbons as high as 1,281 μg/g. In related studies, Betancourt and McLean (1973) found that Bunker C spilled from the *ARROW* weathered only 20 percent after one year in low energy environments as on the shoreline above the limit of wave activity.

Concentrations of aromatic hydrocarbons in California mussels, razor clams, and other invertebrates following the *NESTUCCA* spill were also relatively low. All concentrations were <100 ng/g (dry weight); most concentrations were <45 ng/g (dry weight). These levels generally were as low as the "cleanest" sites sampled as part of the NOAA Status and Trends Program (National Oceanic and Atmospheric Administration 1987). Of the 100 sites sampled routinely, only 26 sites resulted in aromatic hydrocarbon concentrations of <45 ng/g (dry weight) in oyster or mussel tissue. Coastal sites at Cape Flattery and Grays Harbor in Washington, and Coos Bay in Oregon, ranged from 20 to 141 ng/g (dry weight) from 1986 to 1989.

In contrast, Vandermeulen *et al.* (1977) found considerably more oil associated with tissues of bivalves, even seven years after the *ARROW* spill. As determined by fluorescence, clam tissues (siphon epidermis, siphon, mantle, mantle edge) collected from chronically-oiled beaches in Moussiliers Passage in Chedabucto Bay contained relatively high concentrations of aromatic and cyclo-alkane hydrocarbons (93 μg/g, 16 μg/g, 11 μg/g, and 16 μg/g (wet weight), respectively. In follow-on studies, Gilfillan and Vandermeulen (1978) determined by fluorescence that clams from Janvrin Lagoon in Chedabucto Bay also contained relatively high burdens (up to 200 μg/g wet weight) of petroleum hydrocarbons. To explain how oil from the *ARROW* spill could remain bioavailable, even six or seven years after the spill, Vandermeulen and Gordon (1976) hypothesized that persistent hydrocarbon fractions found in clams represented oil that chronically re-entered surficial sediments and interstitial water as leachates from stranded and weathered oil (tar). The assumption was that significant deposits of oil were not cleaned and left to weather naturally.

There are unfortunately few other case histories where the fate of Bunker C fuel oil has been studied, particularly in northern latitudes. There are, however, other relevant data now beginning to emerge from studies of the spill of North Slope crude oil by the *EXXON VALDEZ* in Prince William Sound, Alaska. While comparison to the *NESTUCCA* spill cannot be rigorous, concentrations of total aromatic hydrocarbons in mussels one year after the spill ranged from 235 ng/g to 82,352 ng/g dry weight with a mean of 16,236 ng/g and standard deviation of 28,139 ng/g (Houghton *et al.* 1991). Because many of the study sites are classified as protected, low-energy sites, and much buried oil still exists, sediment-bound oil will likely continue to be available to intertidal resources for a relatively long time.

Factors Influencing Weathering and Depuration

There are likely several factors that accounted for the relatively rapid depuration of oil following the *NESTUCCA* spill including: 1) the time of year in which it occurred, 2) the type of beach or coastline affected, and 3) the timely and efficient clean-up.

Time of Year

Because the spill occurred in winter when water and air temperatures were lowest, much of the oil rapidly congealed into "blobs," "patties" and large "mats" before coming ashore. In some cases, the Bunker C oil from the *NESTUCCA* was at sea from 1-2 weeks before grounding on some of the ONP beaches, and it had weathered significantly during this period. The relatively high sea state at the time of the spill also likely served to enhance weathering; high winds increased evaporation and the resulting high seas increased dissolution and dispersion. This was not the case in every location affected by the spill, however, as shortly after the accident, heavy accumulations of fresh (unweathered) Bunker C came ashore at Ocean Shores and also entered Grays Harbor. Relatively fresh oil also stranded at Whale Creek on the Quinault Indian Reservation and on the more southern

beaches of ONP (Second Beach, Kayostla Beach, Norwegian Memorial North).

Type of Beach

The area of the Washington coast most affected by the spill is characterized by unprotected, high energy, rocky headlands and sand beaches. Fortunately, this type of shoreline tends to cleanse itself most rapidly (Duval *et al.* 1981). Most Bunker C stranding on the rocky shorelines (Kayostla Beach, Norwegian Memorial North, Wedding Rocks) of the Washington coast was removed relatively quickly by wave action and a series of severe winter storms that occurred immediately following the spill. The relatively low concentrations of oil (63 to 250 μg/g by IR), essentially trace amounts, associated with these coastal stations during the third survey, confirmed that weathering and depuration proceeded rapidly. What residual oil remained was restricted to the more protected rock and cobble substrates associated with gently sloping beaches at Kayostla Beach and Norwegian Memorial. The finding of significantly decreased nC_{17}/Pristane and nC_{18}/Phytane ratios associated with the extra sediments collected in the Norwegian Memorial area of ONP also suggested that weathering occurred very rapidly in selected Washington coastal sediments (Table 6).

Although the sand beaches at Ocean Shores (North Jetty area) were heavily oiled, oil was not detected during any of the three surveys conducted at this location, suggesting more rapid depuration from open sand beaches. Polycyclic aromatic hydrocarbons were also mostly undetectable in razor clams and mussels from Ocean Shores. Finally, even though very high concentrations of oil (6,255 and 19,015 μg/g dry weight by IR) were found on Sand Island during the second survey, attempts to relocate this oil during the third survey proved unsuccessful, possibly indicating that weathering and depuration in this habitat proceeded rapidly. Shifts in the configuration of sand dunes on the Island mediated by intense storm events during the winter of 1989-1990 were likely partially responsible.

Efficacy of Clean-up

Finally, clean-up was implemented immediately and was extensive. Clean-up crews worked all affected beaches; only one "set-aside" beach was established in ONP to study potential effects of oiling on intertidal ecology. Absorbent pads were used during the first few days of the spill when the oil was still fresh. Pom-poms were installed and used effectively over cobble substrates containing buried oil at Norwegian Memorial North. Intense winter storms accompanied by extremely high tides at the time of the spill refloated extensive amounts of stranded debris, effectively adding much natural oil-absorbent material to affected waters. Oil in the form of "mats" and smaller "patties" were easily picked-up or scraped-off rocks. Oiled debris consisting of kelp mats, eel grass, driftwood and other flotsam were also removed for ultimate disposal in a certified landfill. Helicopter access to even the most remote beaches on the coast greatly facilitated the clean-up process. Approximately 45,000 yd^3 of oiled logs were also burned on Washington coastal beaches (including those of ONP) following the spill (Lt. M. Smith, Marine Safety Office, U.S. Coast Guard, Seattle District, pers. comm.). Other logs as well as large rocks and boulders were "brush-torched" to remove oil, although this technique had only limited success. Oil adherent to logs and rocks was heated until formation of an ash, but because rocks often exploded during this process, raising concern for operator safety, this technique was discontinued. Propane-fired torches were also used on heavily oiled, cobble beaches of Vancouver Island, but again with little effectiveness (Harding and Englar 1989).

Relatively high concentrations of total oil and grease (30,000 mg/kg by IR) were also significantly reduced by clean-up following the spill of Alaska North Slope crude oil from the *ARCO ANCHORAGE* in Port Angeles harbor in December 1985 (Word *et al.* 1987a, b). Average concentrations of residual oil and grease at the end of an intensive four month clean-up period were 450 mg/kg. The maximum observed average concentration in mixed-soft sediments (0-38 cm in depth) within treated areas was approximately 1100 mg/kg. In contrast, Vanderhorst *et al.* (1981) showed in field experiments that residual Prudhoe Bay crude oil concentrations in intertidal sediments under natural conditions of weathering and depuration decreased from about 2000 mg/kg to undetectable levels within 18.5 months. The Strait of Juan de Fuca and the harbor at Port Angeles can be described as protected, low-energy environments.

Clean-up on Vancouver Island following the *NESTUCCA* spill proceeded in much the same way as efforts along the Washington coast and over essentially the same timeframe. Canadian officials (Harding 1990) also indicated that a rapid and thorough clean-up program following grounding of the oil in early January 1989 served to reduce the impacts of the spill. The grounding of oil in locations where natural self-cleaning was at maximum (high wave action) also limited impacts.

Conclusions

Although relatively high concentrations of oil (6255 and 19,015 μg/g dry weight) were found on Sand Island in Grays Harbor during the second survey, the relatively low concentrations of oil (63 to 250 μg/g dry weight), essentially trace amounts, associated with the coastal sites during the third survey suggest that depuration was relatively rapid and that little oil residual remains from the 1988 *NESTUCCA* oil spill. The relatively low concentrations of aromatic hydrocarbons (mostly <45 ng/g dry weight) found in invertebrates following the spill also represent essentially background levels and indicate that oil was rapidly metabolized and depurated, or is no longer biologically available. These data tend to confirm results of analyses of surficial sediments indicating that little residual oil remains.

Factors likely contributing to the relatively rapid weathering and depuration of oil from impacted beaches include 1) the time of year in which the spill occurred, 2) the type of beach or coastline affected, and 3) the timely and efficient clean-up. Most spilled oil congealed before stranding due to cold air and water temperatures. Large amounts of floating debris also tended to catch (adsorb) significant quantities of oil. The area of the Washington coast most affected is characterized by unprotected, high-energy sand beaches and rocky headlands, which tend to rapidly cleanse themselves. Finally, clean-up was immediate and the congealed oil was easily removed from affected beaches.

Despite our conclusion that little oil remains after the *NESTUCCA* oil spill, the potential for buried, virtually unweathered oil resurfacing on Sand Island and possibly coastal beaches still exists. Sampling on Sand Island and the Washington coast was minimal (one transect per beach), and it is conceivable that surveys conducted by the U.S. Coast Guard, the State of Washington, and others, upon which our survey design was based, could have overlooked some deposits of buried oil. Our conclusions, therefore, should be viewed with that understanding.

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Coho Salmon (*Oncorhynchus kisutch*) Use of Lakes and Streams in the Keogh River Drainage, British Columbia

Abstract

Seasonal patterns of freshwater habitat use by coho salmon were documented in two small watersheds on northern Vancouver Island over a three-year period to assess the importance of small lakes and non-natal tributaries as rearing and over-wintering areas. Spawning occurred at a limited number of locations in these systems. Newly-emerged coho fry moved both upstream and downstream from spawning areas in the Misty Lake system towards Misty Lake. The capture of fry in Long Lake and its outlet stream, where spawning was not observed, indicated upstream dispersion of fry from the Keogh River. The lakes provided both summer rearing and over-wintering habitat for juvenile coho salmon, but their use varied between years. The mainstem Keogh River was used primarily for rearing during summer. Coho fry generally grew fastest in the lakes and their outlet streams. Cohorts of large fry (mean FL $>$ 80 mm) did not show over-winter growth, but the mean sizes of cohorts of small fry (mean FL $<$ 70 mm) increased over winter, suggesting size-differential mortality. The utilization of small tributary lakes and streams as both summer rearing and over-wintering habitat by juvenile coho salmon suggests that more emphasis should be placed on the preservation and management of such areas. Because use of these habitats may be temporally variable, their importance is easily underestimated.

Introduction

In the Pacific Northwest, juvenile coho salmon live in freshwater for one to three years before seaward migration as smolts (McPhail and Lindsey 1970, Drucker 1972). Because of their long period of freshwater residency, patterns of freshwater habitat use are particularly important in the management of coho salmon. However, studies documenting the seasonal importance of various habitat types are uncommon.

The distribution of spawning habitat for coho salmon is often clumped within a watershed, requiring the dispersion of fry away from spawning areas. Major episodes of fry dispersal within freshwater include movements during spring in both downstream (Chapman 1962) and upstream (Gribanov 1948) directions, as well as pre-winter movements into small tributaries and riverine ponds (Skeesick 1970, Bustard and Narver 1975, Peterson 1982). Downstream dispersion in spring may partly result from displacement of fry by larger, social dominants (Chapman 1962, Mason and Chapman 1965). Habitat quality also influences fry density, and thus dispersion, through the relationship between territory size and food resources (Mason 1976a, Dill *et al.* 1981).

The importance of fry dispersal to the production of smolts and adult coho remains largely unknown. In many coastal river systems, significant numbers of fry migrate to sea (Mason 1975, Crone and Bond 1976, Hartman *et al.* 1982), but apparently make little contribution to adult returns (Pritchard 1936, Mason 1975, Crone and Bond 1976). Nomadic fry establish residence where space permits (Chapman 1962), and live in a variety of habitats (Dolloff 1987, Murphy *et al.* 1989). Growth and production vary considerably among habitat types (Bilby and Bisson 1987, Dolloff 1987).

We undertook this study to document seasonal patterns of habitat use by juvenile coho in two small watersheds, one of which was believed to be colonized by fry, and to determine the growth of juvenile coho in stream and lake habitats within the watersheds.

Materials and Methods

Study Site

The use of tributary streams and lakes by coho salmon was examined in the Misty Lake and Long Lake drainages of the Keogh River, a small coastal river on northern Vancouver Island (Fig. 1). Descriptions of the Keogh River watershed and its fish fauna are given in Johnston *et al.* (1986, 1987b), Swales *et al.* (1988), Ward and Slaney (1988), Irvine and Ward (1989), and Bailey and

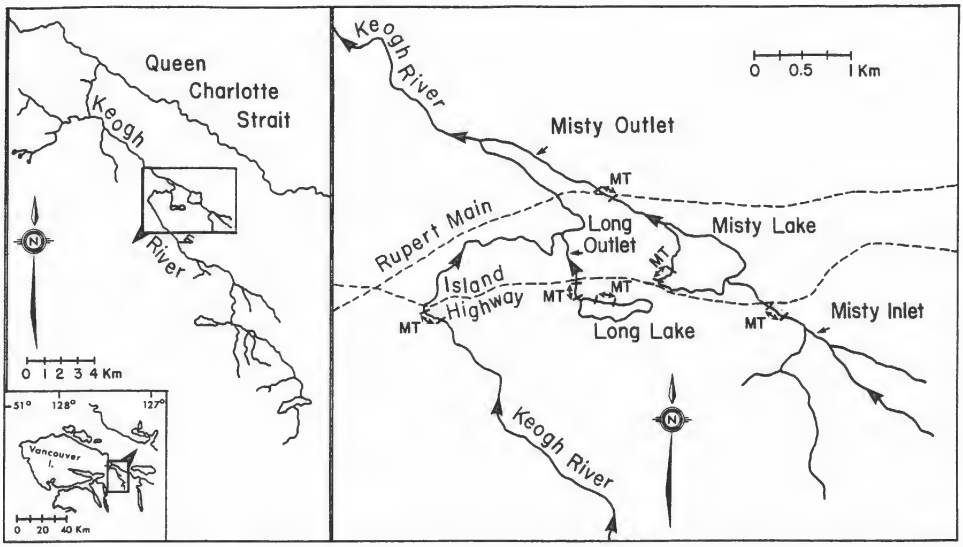

Figure 1. The Keogh River drainage, and the Misty Lake and Long Lake sub-drainages, showing the minnow trapping locations (MT). Large arrows indicate the direction of flow. Insets show the location of the study area within the Keogh drainage and the location of the Keogh River drainage on northern Vancouver Island.

Irvine (1991). The Keogh River is 32 km long and drains a partially-logged, conifer-forested watershed of about 130 km^2. Large flow variations occur during the autumn-winter rainy season. Mean annual discharge is 5.3 $m^3 \cdot s^{-1}$ and mean summer flow is 1.6 $m^3 \cdot s^{-1}$. The maximum estimated flow is 254 $m^3 \cdot s^{-1}$. Between 55,000 and 105,000 (mean = 71,000) coho salmon smolts emigrate from the Keogh River system annually (Irvine and Ward 1989). Other fish species found in the drainage include pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), steelhead and rainbow trout (*O. mykiss*), Dolly Varden char (*Salvelinus malma*), cutthroat trout (*O. clarki*), kokanee (*O. nerka*), coast range sculpin (*Cottus aleuticus*), prickly sculpin (*C. asper*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific lamprey (*Lampetra tridentatus*).

The Misty Lake and Long Lake systems drain into the mainstem Keogh River about 11 km and 13 km upstream of the confluence of the Keogh River and Queen Charlotte Strait (Fig. 1). The Misty Lake watershed comprises Misty Lake and its inlet and outlet streams, Misty Inlet and Misty Outlet. The Long Lake watershed consists of Long Lake and its outlet stream, Long Outlet. The lakes are small and shallow, and the streams are small (Table 1). Riparian vegetation is primarily a shrub community of salal (*Gaultheria shallon*), Red Alder (*Alnus rubra*), and willow (*Salix* spp.). Away from the streambank, the vegetation is dominated by Western Hemlock (*Tsuga heterophylla*), Western Red Cedar (*Thuja plicata*), and Sitka Spruce (*Picea sitchensis*). During summer, canopy closure exceeds 50 percent for each of the streams. Approximately 40 percent of the Keogh River

TABLE 1. Physical characteristics of the Misty Lake and Long Lake sub-drainages recorded during the study.

Parameter	Misty Inlet	Misty Lake	Misty Outlet	Long Lake	Long Outlet
Mean width (m)	2	–	3	–	2
Mean depth (m)	0.5	2.0	0.5	2.5	0.3
Mean velocity ($cm \cdot s^{-1}$)	25	–	45	–	40
Area (ha)	–	25.0	–	8.3	–
Shoreline length (km)	5.3	2.8	2.3	1.8	0.9
Mean gradient (%)	1.5	–	1.0	–	<0.5
Temperature range (°C)	1-19	2-20	2-15	1-19	3-19

watershed has been logged during the past 40 years. Logging has not occurred at any of our study sites although the Misty Inlet watershed upstream of our sampling sites has been logged.

Adult Salmon

To estimate numbers of adult coho salmon, nine visual surveys were conducted during the fall of 1986 in Misty Outlet downstream of the Rupert Main road crossing, and in the 250 m section of Long Outlet upstream of the Island Highway crossing (Fig. 1). The lower-most sections of Misty Inlet also were surveyed periodically. During overview surveys in Misty Outlet upstream of the Rupert Main bridge, and in Long Outlet downstream of the highway crossing, adult coho salmon were not seen and little or no spawning habitat was found. Therefore, regular spawner surveys were not conducted in these regions.

Survey methods for adult coho salmon followed those of Johnston *et al.* (1987a), with either two or three observers walking downstream, using 2 m long poles to probe for fish. Carcasses found were sexed, measured, and slashed to avoid recounting.

Coho escapements were estimated as peak daily counts of live fish, peak daily counts of live fish plus accumulated carcass counts to that date, total carcass counts, and the area under the curve (AUC) of counts of live fish divided by the time in days that fish were estimated to survive in the stream. The AUC estimate used a stream life of 11.4 d obtained from mark-recapture data for Keogh River coho the previous year (Johnston *et al.* 1986).

Juvenile Salmon

Major changes in relative abundance, measured as catch per unit effort (CPUE), and sizes of juvenile coho salmon were estimated with data collected through a standardized minnow trapping program. Misty Inlet, Misty Lake, Long Lake, Long Outlet, and the mainstem Keogh River about 100 m above the Island Highway crossing were sampled at 2 to 4 week intervals from November 1985 to April 1987, and at irregular intervals thereafter to August 1988; Misty Outlet was similarly sampled commencing October 1986 (Fig. 1). Minnow traps were used as they could be deployed by staff who had minimal fisheries training, and also because this technique enabled us to sample pools and areas of dense cover where other techniques were impractical.

The minnow traps and trapping methods were described in detail in Swales *et al.* (1988). On every sampling occasion, between 15 and 35 traps (6 mm mesh, 15 mm diameter opening) were spaced at 3-5 m intervals at each site. Traps were set on the substrate and a rope extended between each trap and the bank. Traps were baited with salmon roe and fished overnight (about 20 h). Swales (1987) showed that minnow trap catches of juvenile coho in the Keogh River drainage increased to an asymptote at about 24 h. According to Bloom (1976), minnow traps are non-selective by size of coho over the range from 51 to 100 mm forklength (FL). In spring 1987, some traps were lined with fine-mesh hardware cloth (1 mm mesh) to retain newly-emerged fry. Fish captured were anaesthetized in 2-phenoxyethanol, FL was measured to the nearest mm, and the fish were released. Age-at-length was estimated from length-frequency analyses (Macdonald 1987), and from scale-aging samples of fish.

The efficiency of minnow traps in capturing juvenile coho may vary both seasonally and among the various habitat types sampled. Therefore, differences in CPUE are not necessarily directly proportional to differences in relative abundance. Nevertheless, the presence of juvenile coho in traps at a particular location confirms the use of that site at a particular time of year. Comparisons between the CPUE and mean sizes of juvenile coho salmon obtained from our minnow trapping and the densities and mean sizes of coho estimated from electrofishing surveys at the Keogh River site (B. R. Ward, B. C. Fisheries Branch, unpublished data), suggest that mean sizes and interannual changes in abundance are adequately represented by the minnow trap data.

To examine the movements of newly-emerged fry, upstream-downstream fry traps similar to those used by Northcote (1969) were operated between 18 March and 13 April 1987 and from 17 March to 13 May 1988 in Misty Inlet and Misty Outlet. Fry traps (1 mm mesh) were operated along the stream margins about 400 m downstream of the minnow trapping sites (Fig. 1). Approximately 20 percent of the stream width was sampled by the traps in each instance. These fry traps were checked daily or on alternate days depending on rate of capture. All coho were counted. Fork lengths were measured on each occasion, to a

maximum of 25 fry moving in each direction at each site. Downstream migrating fry were released at least 1 m below the traps, and upstream migrating fry were released at least 1 m above the traps. In 1988, approximately half the fry captured moving upstream at Misty Outlet were marked (by the removal of the left pelvic fin) to determine if these fry were destined for Misty Inlet. All fry captured at Misty Inlet were examined carefully for clipped fins.

Results

We found adult coho salmon in the lower-most 1.5 km of Misty Outlet from late October until 2 December 1986. Adult coho were never seen in the upper portion of Misty Outlet, in Misty Inlet, or in Long Outlet.

Estimates of the coho escapement into Misty Outlet in 1986 ranged between 31 and 48 fish. The peak daily count was only 25 live fish, but the peak daily count of live fish plus accumulated carcasses was 31 fish, and the total carcass count was also 31 fish. If an observer efficiency for live coho of about 75 percent (Solazzi 1984, Johnston *et al.* 1987a) is assumed, the expanded daily peak count of live fish plus accumulated carcass counts produced an escapement estimate of 39 fish. The AUC estimate was 48 fish.

Newly-emerged coho fry caught in upstream-downstream traps in the Misty Lake drainage in early spring showed directional movement towards the lake (Table 2). Coho fry caught in Misty Outlet were predominantly moving upstream in both 1987 and 1988. In Misty Inlet, migrating fry were only caught in 1988 and were predominantly moving downsteam. These data imply that adult coho spawned in Misty Inlet during the fall of 1987 but not during the fall of 1986. The few parr caught in the upstream-downstream traps in 1988 were also moving upstream in Misty Outlet, but parr movements were random in Misty Inlet. In 1988, yolked fry were caught in Misty Outlet during late March and early April, indicating that fry emergence occurred during this period, while fry emerged slightly later in Misty Inlet (median dates of capture of yoked fry = 9 April and 11 April respectively), and at a slightly smaller size (Table 2, Student's t-test, $p < 0.001$). Few fish other than coho were caught in the upstream-downstream traps.

In 1988, upstream-moving fry at Misty Outlet (mean FL = 40.4 mm) were significantly larger than downstream-moving fry (mean FL = 38.8 mm) (t-test, $p < 0.001$), but upstream- and downstream-moving fry did not differ in size at Misty Inlet (t-test, $p = 0.38$). Although 436 fry migrating up Misty Outlet in 1988 were marked, none of these fry were recaptured in Misty Inlet.

Major seasonal trends in the pattern of habitat use by juvenile coho salmon can be inferred from the minnow trap CPUE data (Fig. 2). Both lakes were used during winter, but the importance of the lakes for summer rearing varied between years. Declining CPUE in Long Lake between late winter and early summer probably resulted from the exodus of coho smolts (Irvine and Ward 1989). All stream sites were used for both summer rearing and over-wintering, although CPUE in the mainstem Keogh River during winter was very low. During summer, CPUE in streams were consistently greater than CPUE for lake sites. Increases at each stream site during the spring of 1987 were the result of catches of newly-emerged fry, more of

TABLE 2. Catches of newly-emerged coho salmon fry and parr in upstream-downstream traps in Misty Outlet and Misty Inlet in spring 1987 and 1988, and the probability of random movement from the binomial distribution.

Year	Site	Mean FL (mm)	Numbers Moving		Probability
			Down	Up	
fry:					
1987	Misty Outlet	35.2 (SD=2.1)	3	55	<0.001
	Misty Inlet		0	0	
1988	Misty Outlet	39.9 (SD=2.4)	213	878	<0.001
	Misty Inlet	38.0 (SD=1.5)	64	17	<0.001
parr:					
1988	Misty Outlet	72.8 (SD=12.1)	7	22	0.004
	Misty Inlet	81.4 (SD=14.2)	10	16	0.163

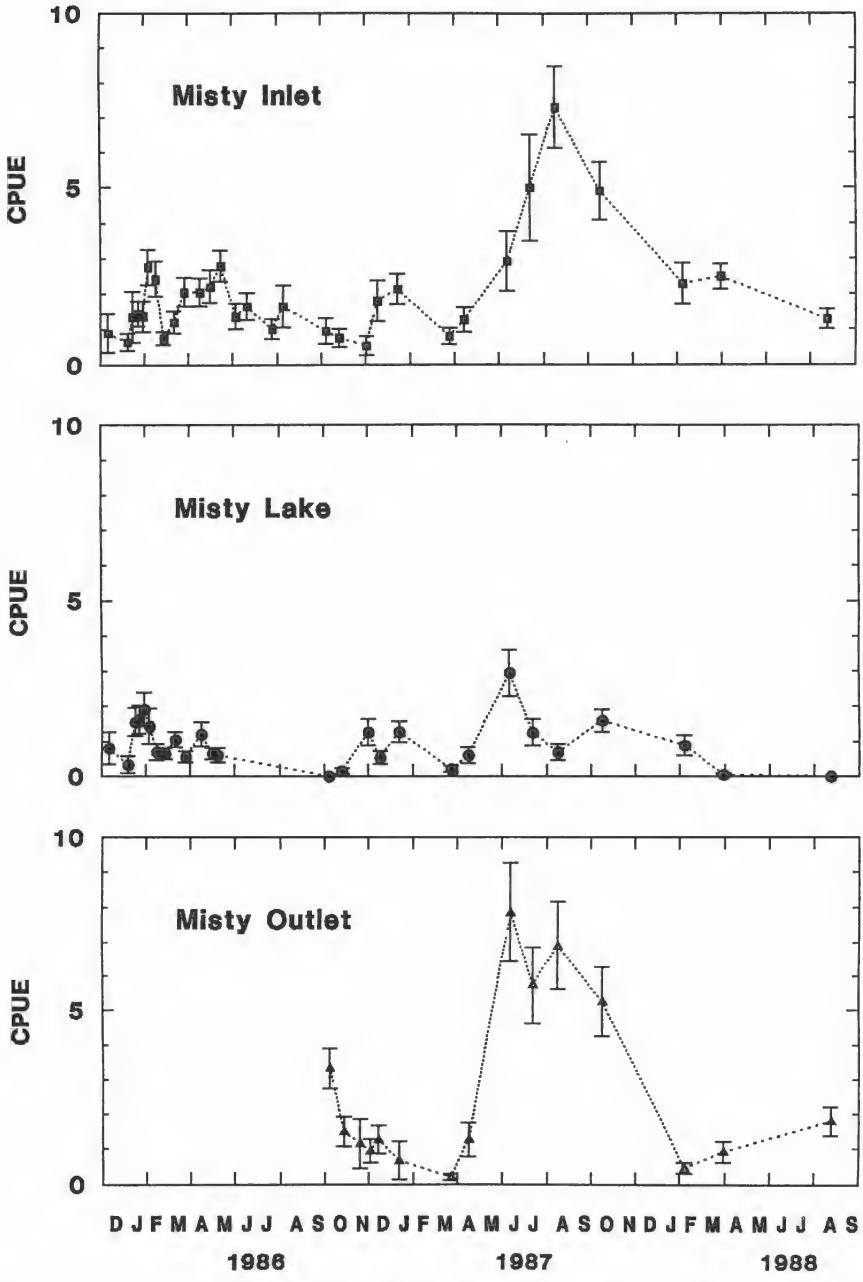

Figure 2(a). CPUE (fish•trap-night^{-1} ± SE) of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage (see next page for continuation of figure). In spring 1987, some traps were lined with fine-mesh hardware cloth which may have increased catches of newly-emerged fry.

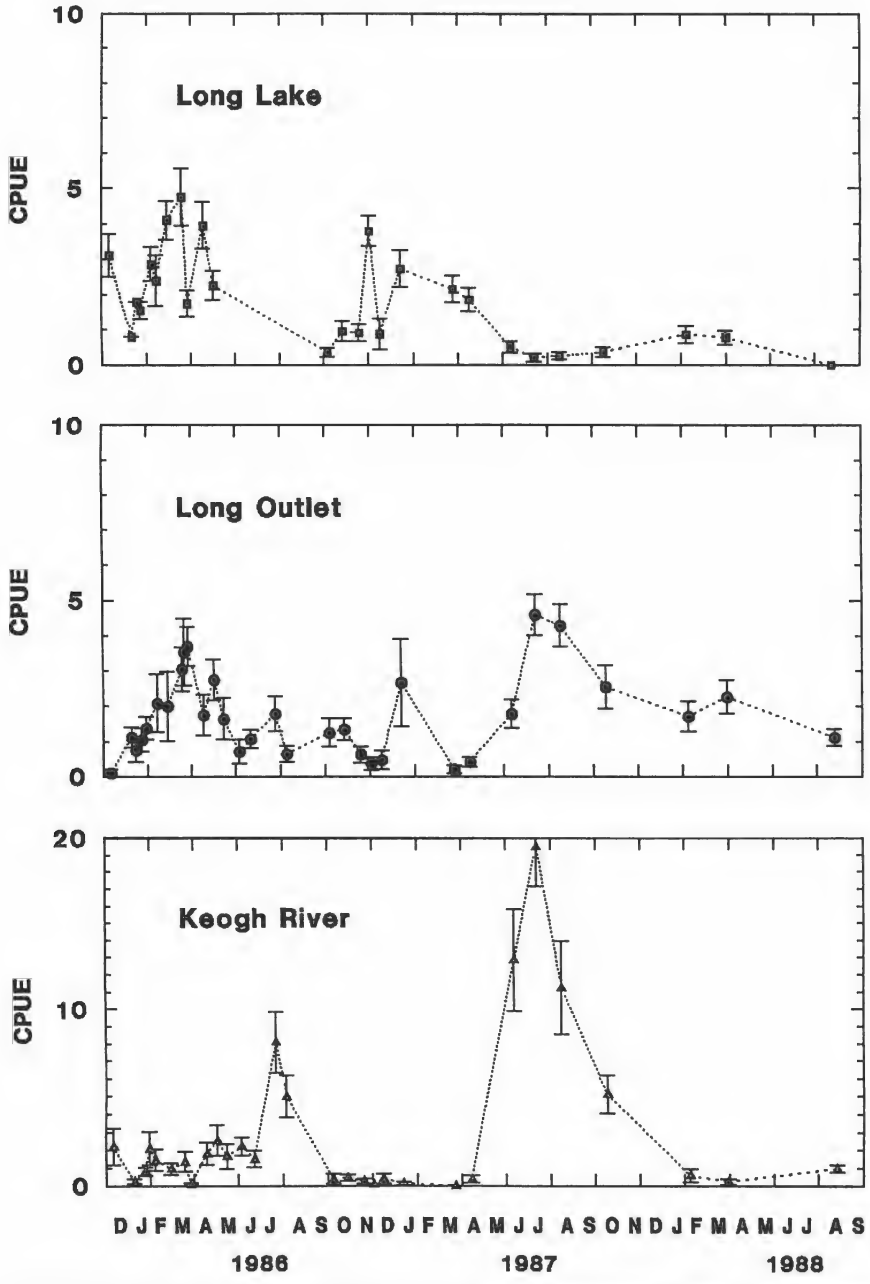

Figure 2(b). CPUE (fish•trap-night^{-1} ± SE) of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage (see previous page for beginning of figure). In spring 1987, some traps were lined with fine-mesh hardware cloth which may have increased catches of newly-emerged fry.

which were retained than in spring 1986 because of the smaller mesh size used in the minnow traps in 1987.

Although coho salmon were generally the most numerous species captured in the minnow traps and the only species for which detailed results are presented in this paper, other species of fish were captured. Rainbow trout were common in samples from the mainstem Keogh River but were rare elsewhere. Dolly Varden char and cutthroat trout were relatively common in Misty Inlet, Long Outlet, and Long Lake but were scarce elsewhere. Threespine stickleback were the most frequently captured fish in Misty Lake, and were also common in Long Lake. Sculpins were occasionally captured at several sites. No evidence of predation on juvenile coho salmon in our minnow traps was seen.

Changes in the mean sizes of coho in the minnow trap catches suggested considerable variation in growth rates among sites and among years (Fig. 3). Growth rates tended to be greatest in the two lakes and their outlet streams. Growth rates were lowest at Misty Inlet, where the size-frequency distributions and scale aging showed two distinct age-groups to be present. The among-site differences in apparent summer growth rates may partly result from differences in water temperature, which were generally higher in the two lakes and lower at Misty Inlet than elsewhere (J. R. Irvine, unpub. data). Growth rates in 1987 were lower than in 1986.

For cohorts of fry whose fall mean size exceeded about 80 mm FL, there was little indication of over-winter growth at any site prior to March-April (Fig. 3). The mean size of smaller fry (<70 mm), however, appeared to increase over the winter despite low water temperatures.

Discussion

Small tributary lakes and stream areas not used for spawning nevertheless are important summer rearing and over-wintering areas for juvenile coho salmon in the Keogh River drainage. Coho fry in two tributaries dispersed from isolated spawning sites to rear in both lake and stream habitats throughout the year.

The mechanisms controlling the directional movement by coho fry towards lakes in the Keogh River drainage are not known. Gribanov (1948) reported coho fry moved 10 to 15 km upstream to reach lakes in which they reared over summer. Mason (1976b) found that fry emerging from simulated redds exhibited a strong upstream response. Upstream movement of coho fry was not found in Carnation Creek, British Columbia (Hartman *et al.* 1982) which lacks tributary lakes. Downstream movements of coho fry soon after emergence are well-known (Chapman 1962, Crone and Bond 1976, Hartman *et al.* 1982), and have been attributed to the aggressive displacement of smaller fry by larger, territorial fry (Chapman 1962, Mason and Chapman 1965, Hartman *et al.* 1982). Downstream displacements of small fry can be induced when coho are stocked at high densities (Mason 1976a, Bilby and Bisson 1987). In contrast, increased food availability may offset the effects of high population density, allowing more fish to coexist (Mason 1976a). Size-based aggressive displacement of fry is unlikely to account for the movements inferred from our fry trap and minnow trap data because the mean sizes of fry migrating upstream towards Misty Lake were the same as or larger than those of downstream-moving fry. Positive rheotaxis (Hoar 1951) cannot be invoked to account for the observed fry dispersal since movement was primarily upstream in Misty Outlet but downstream in Misty Inlet.

Coho fry moved towards lakes in the Keogh River drainage soon after emergence (April), and were found in near-shore lake habitat from early June onward. Other studies have also recorded the presence of juvenile coho in lakes during the summer (Gribanov 1948, Foerster and Ricker 1953, Mason 1974, Russell *et al.* 1981, Hyatt *et al.* 1984, Fielden and Holtby 1987, Swain and Holtby 1989). Large numbers of juvenile coho salmon rear in small lakes in some watersheds. Murphy *et al.* (1989) estimated that about 26 percent of the juvenile coho in the lower Taku River, Alaska reared in beaver ponds. Because juvenile coho in ponds and lakes are most abundant in shallow nearshore areas (Mason 1974, Swales *et al.* 1988, Swales and Levings 1989), the ratio of lake perimeter to stream length can be used as an index of the relative potential importance of these habitats for coho rearing in a watershed.

The apparent growth of coho fry was fastest in the lakes and their outlet streams. Similarly, Fielden and Holtby (1987) found the largest coho at lake sites within the Cowichan River system, British Columbia. Bailey and Irvine (1991) documented significant differences in body

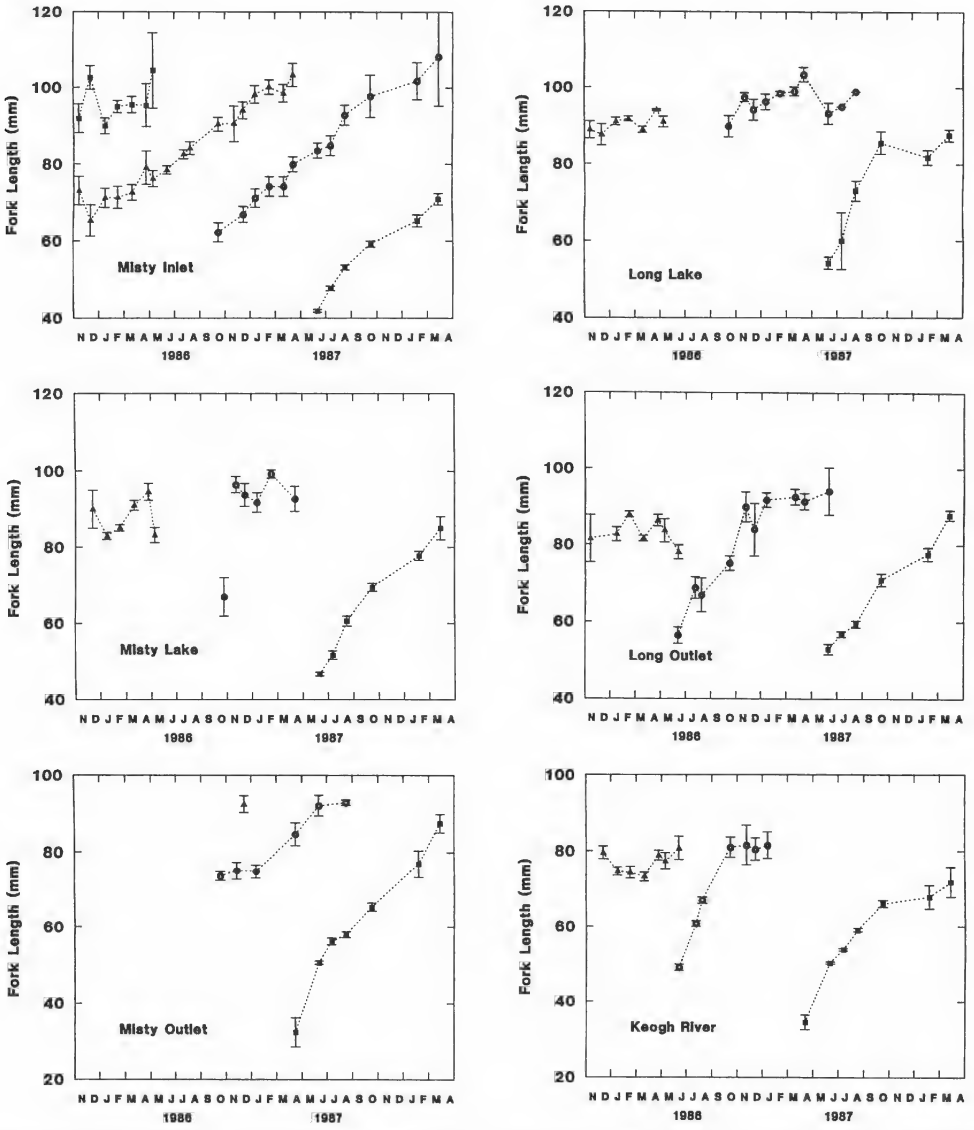
Misty Inlet
Long Lake
Misty Lake
Long Outlet
Misty Outlet
Keogh River
Fork Length (mm)
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1986
1987

Figure 3. Mean FL (±SE) of cohorts of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage. A different symbol is used for each cohort. Small fry were captured during spring 1987 because the minnow traps were lined with hardware cloth.

morphology among groups of coho salmon fry from various riverine environments within the Keogh River watershed. However, they were unable to demonstrate a relationship between the morphology of fish from a particular location, and the habitat characteristics of that location.

The growth rates of juvenile salmonids vary directly with temperature (Iwama and Tautz 1981), and inversely with density (Mason 1976a, Scrivener and Andersen 1984). The higher summer water temperatures and lower relative abundance of coho observed in tributary lakes in the Keogh River

system may permit coho fry rearing in littoral areas to attain larger sizes before winter than stream-rearing fry. Alternatively, fry in lakes may grow quicker because of reduced energetic costs associated with living in environments with minimal current. Large size is adaptive since over-winter survival improves with increased body size in coho (Holtby and Hartman 1982), as does smolt-to-adult survival (Hager and Noble 1976). Growth rate also influences the duration of freshwater residence. The slower-growing coho smolts emigrating from Misty Inlet were comprised of equal proportions of age 1+ and 2+ fish while 91 percent of the faster-growing smolts emigrating from Long Lake were 1+ (Irvine and Ward 1989).

A reduction in CPUE between fall and winter in the Keogh River suggested a movement of juvenile coho out of the mainstem river (Fig. 2). Other studies have documented autumnal migrations of juvenile coho from mainstem rearing habitat into riverine ponds and small tributaries (Skeesick 1970, Bustard and Narver 1975, Peterson 1982, Tschaplinski and Hartman 1983, Swales *et al.* 1986, Brown and Hartman 1988) which are believed to serve as refuges from unfavourable winter conditions such as high discharge, low water temperatures, and reduced food abundance. Low water temperature functions as a cue for juvenile coho to seek areas of low water velocity (Taylor 1988).

Over-winter survival may be greater in lake-fed tributaries than in mainstem rivers because tributaries tend to be less variable. Large increases in discharge in the mainstem Keogh River are associated with winter rains (Ward and Slaney 1988). Fluctuations in water depth were relatively smaller in tributary streams such as Misty Outlet (Johnston *et al.* 1987b, their Fig. 2). Coho fry were virtually absent from the mainstem Keogh River sampling site during winter (Fig. 2), but remained abundant in the lakes and tributaries. Over-winter survivals of 49 to 87 percent have been reported for coho salmon in ponds (Bustard and Narver 1975, Peterson 1982, Swales *et al.* 1986), but survival in stream habitat was much lower (Bustard and Narver 1975). Consequently, small lakes may be major contributors to smolt production in some watersheds. In 1986, Long Lake produced about 1,700 smolts ($0.94 \cdot m^{-1}$ of shoreline) compared to about 765 ($0.14 \cdot m^{-1}$) produced by Misty Inlet (Irvine and Ward 1989).

Swales *et al.* (1986) suggested that coho over-wintering in riverine ponds may continue to grow. Certainly, juvenile coho can feed at low (2.5°C) water temperatures (McMahon and Hartman 1989). Our data showed a continuous increase over the winter in the mean size of cohorts of coho whose initial size was less than about 70 mm FL, but little change in the mean lengths of cohorts whose mean FL was greater than 80 mm. This difference may result from higher over-winter mortalities of the smaller fish. The physiological costs of adaptation to winter conditions are relatively more severe for small coho fry. Mason (1976a) found that coho less than 60 mm FL largely depleted their lipid reserves over winter whereas larger coho lost only a small proportion of their lipid reserves.

The utilization of small tributary lakes and streams as both summer rearing and over-wintering habitat by juvenile coho salmon suggests that more emphasis should be placed on the preservation and management of such areas. Use of these habitats is temporally variable and, therefore, it is easy to underestimate their importance. For instance, adult coho salmon spawned in Misty Inlet during 1987, and have been observed in this stream during other high flow years (P. A. Slaney, B.C. Fisheries Branch, 2204 Main Mall, Vancouver, B.C., pers. comm.), but apparently did not spawn in this stream during 1986. Misty Lake was more important for juvenile coho salmon during the summer of 1987 than the summer of 1988. To protect and manage the freshwater environment of coho salmon, it is necessary to improve our understanding of the complex patterns of freshwater use of this species.

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Agroclimatic Zones for Dryland Winter Wheat Producing Areas of Idaho, Washington, and Oregon[1]

Abstract

There is a need to develop a series of "zones" to facilitate technology transfer within the Intermountain Northwest. Six agroclimatic zones have been delineated based on three climatic and soil parameters important in growing winter wheat: soil depth, mean annual precipitation, and cumulative growing degree days from 1 January through 31 May. Thus each zone, regardless of the state in which it is located, has similar soil and climatic conditions. There are uncultivated areas within each zone that are not identified but if farmed would be farmed like other parts of the same zone. The zones provide a common basis for identifying areas where successful exchange of practices, experience, and knowledge between and among producers, researchers, extension, and Soil Conservation Service personnel will most likely occur. Management decisions that produce desired results in one zone in one state will probably succeed in that same zone in any other state. Conservation practices and erosion control techniques should be similar within but not between zones.

Introduction

New farming technologies have been developed over the last 10 years in the Pacific Northwest (PNW) as a result of a three-state (Oregon, Idaho, and Washington) research effort called Solutions to Erosion and Economic Problems (STEEP) established to develop new erosion control strategies (Oldenstadt *et al.* 1982). However, evaluation and adoption of these technologies have lagged behind the research phase of development partially because of insufficient technology transfer. Producers are hesitant to adopt practices developed in another state or area even if their local soil and climatic conditions are similar. There are few published aids establishing locations of similar soil and climate in this diverse region. Successful management of conservation tillage systems, for example, may benefit from application of available technologies from research done in geographically different locations that have similar agronomic parameters.

This paper describes a series of agroclimatic zones (AZ) delineated on the basis of similar soil and climatic factors in the Intermountain Northwest (Idaho and those parts of Oregon and Washington east of the Cascade Mountains). Objectives were to develop a series of zones for the PNW that would allow scientists, field personnel, and producers to compare new technologies more effectively, to design farm management systems by adapting methods tested in plots located in other areas with similar soil and climatic conditions, and to present their research findings for use in a variety of farming situations.

Criteria Used to Define Agronomic Zones

Criteria used to define and delineate AZ are based on soft white winter wheat, the major crop grown in the Intermountain Northwest. Initial evaluation of criteria needed to effectively delineate zones was done in a five county area in northcentral Oregon (Douglas *et al.* 1988). Only three criteria [soil depth (SD), mean annual precipitation (MAP), and cumulative growing degree days (CGDD) from 1 January to 31 May] were needed to identify six zones that delineated management systems for winter wheat production with regard to erosion control and sustained productivity. The same three criteria were used to delineate these same six zones for the Intermountain Northwest (Douglas *et al.* 1990).

The first criterion used to define AZ was SD. Soil depth is important because it affects soil water storage capacity. Soil depths were determined from published SCS County soil surveys. Most agricultural soils in the Intermountain Northwest have medium textures and thus have the potential to store similar amounts of available water per unit

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depth of soil [approximately 50 mm (2 in) per 0.3 m (12 in) soil]. Much of the precipitation falls during winter when evaporation is low and storage potential is high. Observing appropriate water conservation practices can result in storage of approximately 70 percent of the winter precipitation (Ramig and Ekin 1991). For example, if annual precipitation is 300 mm (12 in), approximately 70 percent or 210 mm (8.4 in) will fall during the winter months, of which 70 percent or 147 mm (5.9 in) could be stored. This amount of water will recharge a medium textured soil to a depth of approximately 1 m (40 in). Soils deeper than 1 m (40 in) will require more than one winter's precipitation to recharge the profile unless annual precipitation is greater than 400 mm (16 in). Thus, two SD categories (Figure 1) were used to define AZ: less than 1 m (shallow) and greater than 1 m (deep).

Water is the single most limiting factor for dryland crop production in the Intermountain Northwest. Thus, the second criterion for segregating land areas into zones was MAP (Figure 2). Mean annual precipitation was determined from National Weather Service 30 year precipitation records, and was used to subdivide cropping areas into three classes: wet, dry, and very dry. The wet class consisted of areas receiving over 400 mm (16 in) of annual precipitation. These areas normally receive sufficient rainfall to support annual cropping of cereals irrespective of SD. The dry class [250 to 400 mm (10-16 in) annually] was chosen to identify areas where SD is important in managing stored soil water. This "dry" area was subdivided into two subclasses: 250-350 mm (10-14 in) and 350-400 mm (14-16 in). Shallow soils (<1 m) are fully recharged almost every winter in both subclasses and can produce a crop annually. Deep soils (>1 m) in the drier subclass do not fully recharge each season and are usually summer fallowed to maximize crop production and water use efficiency. Deep soils in the wetter subclass recharge in most years and can produce a crop annually approximately 70 percent of the time, i.e., seven years out of 10 (personal communication Dr. R. E. Ramig, USDA-ARS, Pendleton, Oregon). These soils can be annually cropped when wetter conditions prevail and summer fallowed when conditions are drier. The very dry class [<250 mm (10 in)] was selected to identify the approximate lower limit of dryland winter wheat production.

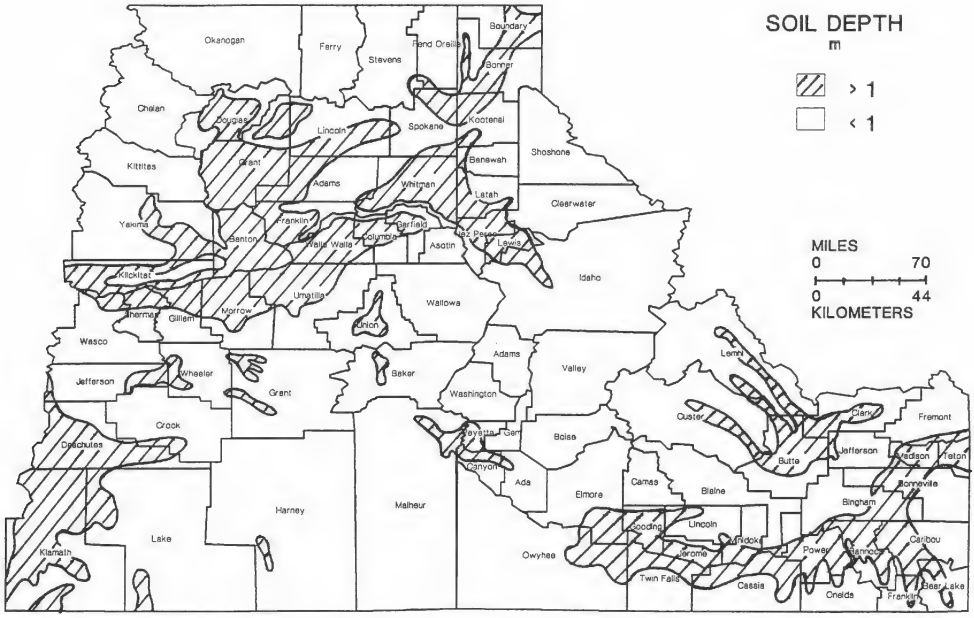

Figure 1. Soil depths for the Intermountain Northwest (m).

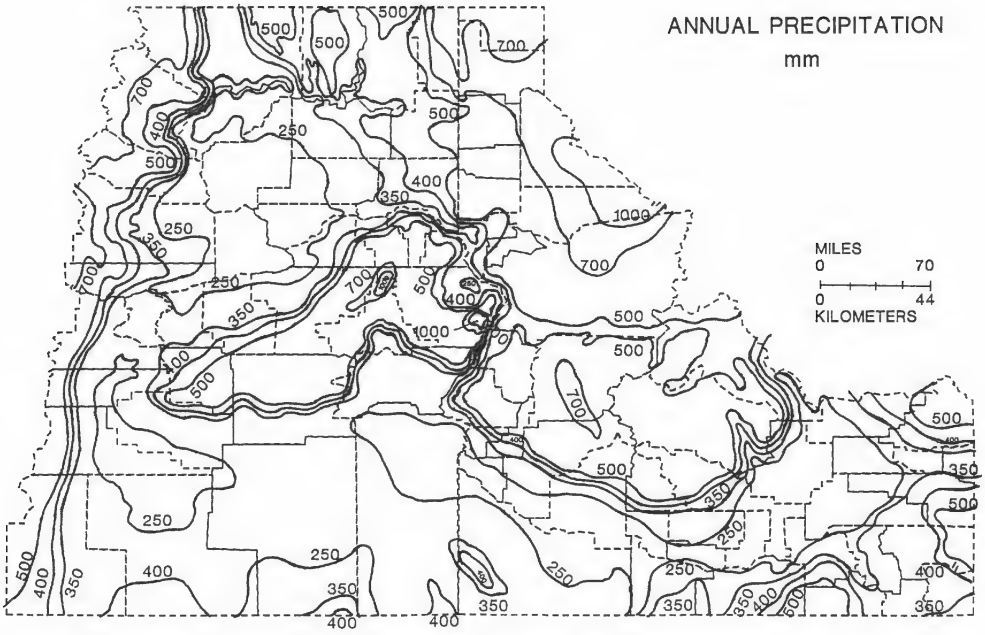

Figure 2. Annual precipitation isohyets for the Intermountain Northwest (mm).

Areas in this class not only receive very little precipitation, they have very high evapotranspiration rates.

The third criterion used to define AZ was CGDD from 1 January through 31 May. Winter wheat growth and management practices in a five-county area in northcentral Oregon were observed and CGDD were determined that fit these observed management patterns (Douglas *et al.* 1988). CGDD were calculated for each weather station by averaging daily maximum and minimum Celsius temperatures, setting negative values (below the freezing point) to zero, and summing for each day from 1 January through 31 May. National Weather Service 30 year temperature records were used to make the calculations.

Three classes were recognized <700 (cold), 700-1000 (cool), and >1000 (warm). CGDD from 1 January-31 May are shown in Figure 3. Figure 3 was constructed from CGDD values for 102 weather stations in the three state area. Values range from a low of 122 in western Klamath Co., Oregon, elevation 1974 m (6475 ft), to 1297 in northern Wasco Co., Oregon, in the Columbia River Canyon, at an elevation of 85 m (280 ft). Values in Idaho, southern Oregon and northern Washington are generally lower than in the rest of the region because of the larger percentage of high elevation land in these areas. The higher values occur in river valleys of the Snake and Columbia Rivers.

In areas receiving <700 CGDD, there is danger of frost in any month, the growing season is short, and evapotranspiration is relatively low. Soil frost damage is generally minimized due to the insulating qualities of a deep, continuous wintertime snowpack, and the thawing of soils frozen prior to the first snowfall by residual soil heat. However, growers must use cereal varieties that are frost tolerant and resistant to snow mold and other pathogens that thrive in cold, moist conditions. The geographic area covered includes most of Idaho, except for the warmer, lower elevation Snake River valley system, southwestern and northeastern Oregon, and northern Washington.

In areas receiving between 700 and 1000 CGDD, winters are sufficiently cold that grains must have some frost hardiness, but the principal frost damage comes from brief, severe, cold periods when there is no snow cover. These areas are prime wheat growing areas with cool temperatures, adequate moisture, and moderate evapotranspiration.

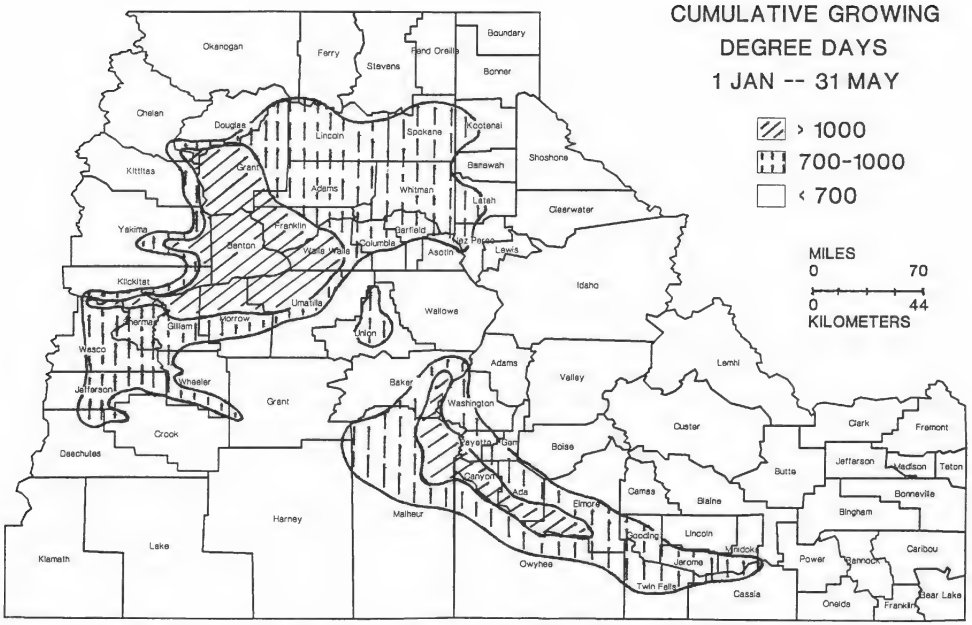

Figure 3. Cumulative growing degree days from 1 January through 31 May for the Intermountain Northwest.

These conditions prevail over a large acreage in central Washington and in narrow bands crossing north-central Oregon, southeastern Idaho, and west central Idaho.

Areas receiving over 1000 CGDD have very warm growing conditions, high evaporative demand, rare frost damage, and a high probability of heat stress after boot stage. Generally early-maturing varieties of wheat are most successful in this area because grain filling occurs before the high summer heat stress begins. This area covers a banana-shaped band running through parts of Grant, Adams, Franklin, Benton, Yakima, and Walla Walla counties in southcentral Washington, and Umatilla, Morrow, and Gilliam counties in northcentral Oregon (Figure 3). There are small elongated bands in southwestern Idaho and in eastern Oregon paralleling the Snake River.

Agroclimatic Zones

Six agroclimatic zones (Figure 4, Table 1) have been delineated based on differences in SD, MAP, and CGDD. These zones have been defined to facilitate technology transfer and application of conservation farming technologies in the Intermountain Northwest. For this reason the discussion of soils in each zone is concerned primarily with those used for cultivation. Vast areas of the Intermountain Northwest are not suited to cultivation and soils of these non-cultivated areas may be very different from the cultivated soils. Sources of soils information for each zone include Boling (1988); USDA Soil Conservation Service (1984 and 1986); and numerous SCS county soil surveys. Many of the areas are still covered with forests and rangelands but if cultivated would be farmed like other parts of the same zone. These uncultivated areas are not identified within each AZ.

Zone 1: ANNUAL CROP-WET-COLD
SD: depth not a factor
MAP: >400 mm (16 in)
CGDD: <700

Zone 1 (Figure 4, Table 1) comprises areas of high elevation and mountainous terrain. Most soils are not suited for cultivation and are marginal for crop production because they are too shallow, too steep, or too cold. Cultivated soils occupy intermountain valleys or mountain foothills and occupy less than 20 percent of the area. In northern Washington and Idaho, soils of this zone are mostly

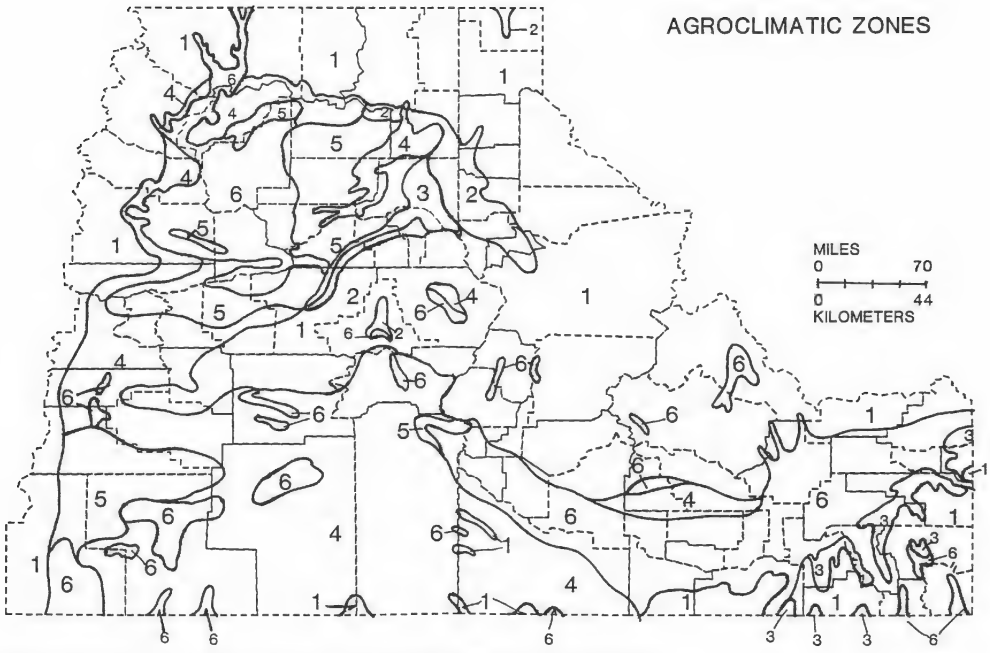

Figure 4. Agronomic zones for the Intermountain Northwest (See Table 1 for legend).

TABLE 1. Agroclimatic zone legend for Figure 4.

Zone	Name	Mean Annual Precipitation (mm)	Soil Depth (m)	Cumulative Growing Degree Days (1 Jan-31 May)
1	ANNUAL CROP-WET-COLD	Over 400 (16 in)	–	Under 700
2	ANNUAL CROP-WET-COOL	Over 400 (16 in)	–	700-1000
3	ANNUAL CROP-FALLOW-TRANSITION	350-400 (14-16 in)	Over 1	700-1000
4	ANNUAL CROP-DRY	250-400 (10-16 in)	Under 1	Under 1000
5	GRAIN-FALLOW	Under 350 (14 in)	Over 1	–
6	IRRIGATED	–	–	–

glacial, glaciofluvial, lacustrine or alluvial in origin. Frequently, the upper profile is formed in a thin, less than 0.5 m (20 in), layer of loess and volcanic ash. These soils are predominantly Xerochrepts with frigid or mesic temperature regimes, with some Andepts and Mollisols. They are coarse to medium textured and level to steeply sloping. Representative series are Waits, Nevine, and Spokane.

Soils of the hills and foothills of the Blue Mountains of Oregon and Washington have formed in loess, residium, and colluvium, have moderate to high amounts of organic matter in the surface, are medium to fine textured, and are gently to very strongly sloping. Most of the soils are Argialbolls or Argixerolls with mesic or frigid temperature regimes. Representative series are Waha and Cowsly.

Soils along the eastern side of the Cascade Mountains are composed of a mixture of parent materials including volcanic ash, loess, and alluvium. They are level to strongly sloping, medium to moderately fine textured, and contain moderate to high amounts of organic matter. Most are Xerochrepts, Xeralfs, and Argixerolls with mesic temperature regimes. Representative series are Goldendale, Gunn, and Wamic.

Native vegetation is primarily dry to moderately dry coniferous forest or PNW bunchgrass types, except in the southeastern part of Idaho where it is shrub-steppe. The primary species in these forests are ponderosa pine (*Pinus ponderosa* Lawson & Lawson), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and grand fir (*Abies grandis* (Don) Lindley) at higher elevations. Lower elevations, which comprise most of the cropped areas in this zone, consist of open forests of ponderosa pine in a woodland savannah-type vegetation (Franklin and Dyrness 1973). In southeastern Idaho, precipitation patterns include more summer rainfall and water storage is less efficient. Thus the cold high elevation land receives more than 400 mm (16 in) of precipitation, but the vegetation is a shrub-steppe dominated by big sagebrush (*Artemisia tridentata* Nutt.) with bunchgrasses such as *Festuca idahoensis* Elmer and other grasses and forbs in the understory (Franklin and Dyrness 1973).

Snow cover in this zone helps decrease winter injury to plants. However, cereal varieties that exhibit the most resistance to snow mold must be planted. There are a few areas in zone 1, especially in eastern Idaho and at very high elevations, where winter cereals cannot be grown because the weather is too cold.

ZONE 2: ANNUAL CROP-WET-COOL
SD: depth not a factor
MAP: >400 mm (16 in)
CGDD: <700-1000

Soils in zone 2 (Figure 4, Table 1) are deep (>1 m [40 in]) and are ideally suited to crop production. Approximately 95 percent of the area is cultivated. Soils are almost entirely formed in deep loess, with minor amounts of alluvium and eolian sand. This zone includes the most productive soils of the region. However, they are very susceptible to water erosion. In Washington and Idaho this zone contains the area commonly known as the "Palouse." Loess can exceed thicknesses of 60 m (approximately 200 ft), especially in Whitman County, Washington (Gentry 1974). In Washington, Oregon (Umatilla County), and Idaho (Benewah and Latah Counties), soils are medium to moderately fine textured, moderate to high in organic matter, and nearly level to steeply sloping. Most soils in this part of the zone are Haploxerolls, Argixerolls, and Argialbolls with mesic temperature regimes. Representative series are Palouse, Athena and Thatuna. In Nez Perce and Lewis counties in Idaho soils are slightly higher in organic matter and have B horizons that are finer textured than the other areas of this zone. These soils are Argialbolls, Palexerolls, and Argixerolls. Nez Perce is a representative series. In the Grand Rhonde valley (Union County), Oregon, the soils are developed from loess, eolian sands and alluvium. The loess soils are similar to those found in the other areas of this zone. The alluvial soils in this valley are high in organic matter and commonly have poor drainage. They are classified as Haploxerolls and Haplaquolls. Alicel and Catherine are representative series.

Zone 2 includes wetter parts of the steppe land originally in the Palouse and Nez Perce prairies. Dominant perennial grass species include bluebunch wheat grass (*Agropyron spicatum* (Pursh) Scribner & J. G. Smith), Idaho fescue (*Festuca idahoensis* Elmer), and a variety of forbs (Daubenmire 1969). This zone receives slightly less precipitation than zone 1, but still greater than 400 mm (16 in) annually. Elevations are generally lower than in zone 1 and temperatures are slightly warmer; thus CGDD are higher (700-1000). However, with the intermittent snow cover, potential for winter injury still exists.

ZONE 3:ANNUAL CROP-FALLOW TRANSITION
SD: >1 m (40 in)
MAP: 350-400 mm (14-16 in)
CGDD: 700-1000

Zone 3 (Figure 4, Table 1), of which 90-95 percent is cropland, identifies areas of deep soils that occasionally have less than adequate precipitation for optimum crop production. Major soils have formed in loess and are medium to moderately fine textured with moderate amounts of organic matter. Landscapes are gently to strongly sloping. In Washington and Oregon these soils are classified as Haploxerolls and Argixerolls with

mesic temperature regimes. Representative series are Walla Walla, Athena, and Broadax. Soils in southeast Idaho are Haploxerolls and Argixerolls with mesic and frigid temperature regimes. A representative series is Rexburg.

Zone 3 comprises land in the Palouse and Nez Perce prairies at slightly lower elevations than zone 2. In southeastern Idaho, it includes shrub-steppe vegetation characterized by an overstory of *Artemisia tridentata* Nutt. and bitterbrush (*Purshia tridentata* (Pursh) DC) interspersed with an understory of forbs.

ZONE 4: ANNUAL CROP-DRY
SD: <1 m (40 in)
MAP: 250-400 mm (10-16 in)
CGDD: <1000

Zone 4 (Figure 4, Table 1) identifies areas with soils that are generally less than 1 m (40 in) thick over bedrock or a restricting layer. Approximately 50 percent of the area is cultivated. Soils in this zone are developed in loess, glacial till and alluvium. They vary widely in texture, and some contain moderate amounts of coarse fragments. Soils of cental and southeastern Washington are developed in loess, glacial till or alluvium with basalt or a restricting layer at a shallow (<1 m) depth. These soils are Haploxerolls and Durixerolls with frigid and mesic temperature regimes. Representative series are Ritzville and Willis. In Oregon (Wasco, Sherman, Gilliam, and Morrow counties), and Washington (Klickitat county), soils are developed in loess over basalt or indurated hardpan. These soils classify as Haploxerolls, Durixerolls, and Argixerolls with mesic temperature regimes. Representative series are Morrow, Willis, and Condon. Soils in central and southern Oregon have developed in loess and alluvium over indurated hardpan, basalt, or other rock. These soils are classified as Durixerolls, Durargids, and Camborthids. Madras is a representative series.

Zone 4 receives 250-400 mm (10-16 in) precipitation yearly and is warm (generally 700-1000 CGDD but can be <700) with shallow soils, therefore, many vegetation types are included. Much of central Oregon, near the Cascade Mountains, is covered with dry, open, ponderosa pine or juniper forests. These areas grade into shrub-steppe and steppe vegetation often dominated by sagebrush (*Artemisia tritendata* Nutt.) and blue bunch wheatgrass (*Agropyron spicatum* (Pursh) Scribner & J. G. Smith). Sandier areas have indian ricegrass (*Oryzopsis hymenoides* (Roemer & Schultes) Ricker) and needle and thread grass (*Stipa comata* Trin. & Rupr.). Sandberg bluegrass (*Poa secunda* J. S. Presl) is common on rockier outcrops (Daubenmire 1970).

ZONE 5: GRAIN-FALLOW
SD: >1 m (40 in)
MAP: <350 mm (14 in)
CGDD: not a factor

Zone 5 (Figure 4, Table 1) identifies areas of deep (>1 m [40 in]) soils that receive limited rainfall (350 mm [14 in] or less). In Washington, and adjacent areas of Oregon, approximately 90 percent of this zone is cultivated. Soils are formed in deep loess, are low in organic matter, and are medium textured. These soils are very susceptible to wind and water erosion. Landscapes are gently sloping to moderately steep. Soils are Camborthids and Haploxerolls with mesic temperature regimes. Representative series are Shano, and Walla Walla. In Klamath, Lake, and Deschutes counties in Oregon, less than 20 percent of the zone is cultivated. Soils are formed in volcanic, alluvial, and lacustrine material. These soils are classified as Haploxerolls and Argixerolls. Representative series are Deschutes and Fordney.

Vegetation in this zone is primarily shrub-steppe in Washington and northcentral Oregon but ponderosa pine and juniper occur on the pumice soils in south-central Oregon near the high Cascades.

ZONE 6: IRRIGATED
SD: depth not a factor
MAP: not a factor
CGDD: not a factor

Zone 6 (Figure 4, Table 1) identifies areas that usually cannot be cultivated without irrigation There are also relatively small irrigated areas in all other zones from 1 through 5.

Native vegetation in zone 6 is generally steppe or shrub-steppe dominated by perennial shrubs and grasses. Soils are coarse to moderately fine textured, low in organic matter, and level to gently sloping. Many are gravelly to very gravelly. In Washington and Oregon, these soils are formed in eolian sands or silty alluvium. They are classified as Torripsamments or Camborthids with mesic temperature regimes. Representative series are

Quincy, Winchester, Sagehill, and Warden. Soils in southern Idaho are formed in loess or alluvium and are classified as Camborthids, Paleargids, Durorthids, Calciorthids, or Haplargids with mesic temperature regimes. Representative series are Gooding, Power, Minidoka, Trevino, and Portneuf. South-central and south-eastern Oregon soils are formed in thin loess and alluvium. They are Haploxerolls, and Durorthids with mesic temperature regimes. Representative series are Fordney, and Nyssa.

Discussion

The dryland Intermountain Northwest, which has a wintertime precipitation regime, is dependent primarily on soil water storage for crop growth. There must be enough water stored over winter, or over two winters, to supply the growing crop during the essentially rainless summer months. Since the major crop grown in the dryland areas of the Intermountain Northwest is winter wheat, we based the delineation of AZ on climatic and soil parameters important in winter wheat growth.

Cumulative growing degree days provide a reliable index to plant development (Rickman *et al.* 1985). The appearance of each successive leaf on the main stem of wheat is linearly related to CGDD with approximately 100 CGDD required for the development of each leaf. Tillers also appear in the same regular pattern at predictable intervals relative to main stem leaf number (Klepper *et al.* 1982). Dates of 1 January to 31 May were chosen for the accumulation of degree days because all winter cereals, regardless of planting date, pass through this time interval. Many of the important temperature-sensitive, yield-determining growth events, such as number of heads per unit of land surface, number of spikelets per head, number of kernels per spikelet, and size and vigor of the last three leaves on each culm, occur during this period.

Since water is the basic resource and is limiting for crop production, AZ can be used to assess the potential for other winter crops such as barley or rapeseed. Most of zone 1 is actually forest and much of zones 4 and 5 is presently rangeland. Forest and rangeland is not delineated, but is included in the zone in which it would fit if it were cropped. These six AZ for the intermountain Northwest may not be useful where wintertime rainfall is not predominant and crops do not depend on soil moisture stored overwinter. However, criteria and concepts should be expandable to develop similar zones in other dryland agricultural areas.

Zones 1 and 2 differ only in CGDD; <700 and 700-1000, respectively. Erosion by water is severe in both zones and annual cropping should be practiced to decrease the erosion potential. Annual cropping helps deter soil erosion by water by keeping the soil surface covered for longer periods of time than if summer fallow was used. Some form of chisel tillage may help increase water infiltration, and subsequently decrease surface water movement down slopes, during winter and early spring in heavy frost areas of eastern Idaho (Massee and Siddoway 1969).

Zone 3 differs from zone 2 in that it is drier (350-400 mm [14-16 in] MAP), therefore, is marginal for annual cropping. Annual cropping can be done approximately 70 percent of the time (personal communication, Dr. Robert Ramig, USDA-ARS, Pendleton, Oregon). In some years annual precipitation will recharge the deep profiles but in drier years it will not. Even though zone 3 falls within the 700-1000 CGDD zone as does zone 2, it requires more careful attention to water management than do either zones 1 or 2.

Zone 4 has very little annual cropping being practiced at this time. However, because soils are <1 m (40 in) to bedrock or an impermeable layer, they are normally recharged completely with one winter's precipitation. Annual cropping would result in more efficient soil water use and reduced soil loss to water erosion. Consequences of erosion are very serious because soils are already shallow. Fallowing almost always guarantees soil loss by water erosion every crop year. Some years, timing of precipitation is such that rains do not begin until it is too late in the fall for germination and emergence of winter cereals before winter. Rotations including early seeded spring cereals would be ideal for this zone.

There is a slight MAP difference between zones 4 and 5 (Table 1) but the major difference is in SD. Zone 5 has deep soils (>1 m), precipitation is low (<350 mm), and the soil profile is not recharged with water in the first winter following harvest, as are soils in zone 4. Temperature is not a factor in this zone as precipitation is dominant. Therefore, the recommended rotation is crop-summerfallow which allows for improved recharge of soil water and maximum water use by the crop.

Soil erosion by water during the summer-fallow season, although severe, is not as severe as summerfallow in zone 4.

Large areas of zone 6 in southcentral Washington and southern Idaho have within their boundaries areas receiving <250 mm (10 in) precipitation that utilize a grain-summerfallow rotation. These are usually areas of silt loam soils that because of the low MAP produce very low grain yields (1.3-1.7 Mg ha^{-1} [20-25 bushel $acre^{-1}$] every other year). Less than 20% of this zone is cropland. Much of zone 6 receives less than 250 mm (10 in) of precipitation annually and has a very high evaporation rate.

Major Land Resource Regions (MLRR's) and Major Land Resource Areas (MLRA's), in another land use classification system (USDA 1981), have been in widespread use for resource planning for farming, ranching, forestry, engineering, recreation, and other uses. MLRA's are geographically associated land resource units "characterized by a particular pattern of soils, climate, water resources, and land uses" (USDA 1981). MLRA's were designed to help "make decisions about national and regional agricultural concerns, identify needs for research and resource inventories, provide a broad base for extrapolating the results of research within national boundaries, and serve as a frame-work for organizing and operating resource conservation programs. Identification of these large areas is important in statewide agricultural planning and has value in interstate, regional, and national planning" (USDA 1981). Agroclimatic zones (Figure 4, Table 1) are different from MLRA's in that they are associated land areas characterized by particular patterns of SD, MAP, and temperature, that require similar management practices for production of winter cereals in Idaho, Oregon, and Washington. They are important in local, intrastate, and inter-state technology transfer and planning, and provide a base for extrapolating the results of research and farming practices across state boundaries. They provide a common basis for identifying areas where successful exchange of practices, experience, and knowledge will be most likely between and among producers, researchers, extension, and Soil Conservation personnel. Each zone has approximately the same climatic and soil depth conditions regardless of the state in which it is located, and decisions that produce the desired results in one zone in one state should work in the same zone in any other state. Conservation tillage practices and erosion control techniques should be similar within but not between zones.

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Analysis of the Biotic Factors Affecting the Seed Set of a Rare Pacific Northwest Endemic: *Sidalcea malvaeflora* (D.C.) Gray ex Benth. *elegans* (Greene) C.L. Hitchc.

Abstract

Populations of *Sidalcea malvaeflora* ssp. *elegans*, a plant on the Oregon Natural Heritage Data Base's 1987 Review List, were investigated to determine factors that limit its seed production.

Viable, undeveloped and weevil damaged seeds from 100 racemes were monitored throughout the reproductive cycles of 1987 and 1988. Experiments were conducted to examine potential limitation to seed production: hand cross-pollinations tested pollen limitation and water/nutrient treatments tested resource limitation.

Production of viable seed was low (3.3% of total ovules in 1987 and 7.1% in 1988), although 16.9 percent and 15.1 percent of ovules (in 1987 and 1988 respectively) had dispersed before collection and could have contributed to viable seed set. The high incidence of undeveloped (aborted or unfertilized) ovules (41.1% in 1987 and 51.5% in 1988) suggested seed set was limited. Seed production was reduced by weevil predation (by 38.7% of all ovules in 1987 and 26.5% in 1988). Viable seed production in hand pollinated fruit was higher than in insect pollinated fruit. Racemes receiving extra water produced more viable seeds than controls. Resource availability and insufficient pollination appear to affect seed production in *S. malvaeflora* ssp. *elegans*.

Introduction

The intensive study of rare and endangered plant species is a relatively new scientific pursuit. In plants which have a low reproductive output, it is necessary to manipulate experimentally, not simply monitor, populations. Such experiments in the field provide the best evidence for factors that may crucially limit rare plant populations. Moreover, without such experimental evidence, legal protection by the state is impossible. Oregon Senate Bill 533, passed in 1987, states that to make a determination on a species' endangerment the reproductive potential must be in danger of failure due to (1) limited population numbers, (2) disease, (3) predation, or (4) other natural or man-made factors affecting continued existence. Moreover, such data help tailor management plans on a species by species basis.

Data collected in 1987 showed that *Sidalcea malvaeflora* (D.C.) Gray ex Benth. ssp. *elegans* (E.Greene) C. L. Hitchc. plants produced many more flowers than fruits (and thus seeds). Predation, pollination limitation, and resource limitation are some of the many hypotheses explaining why plants may produce more flowers than fruits (Stephenson 1981, Horvitz and Schemske 1988). The purpose of this study is to determine which of the above three factors play a part in limiting seed set in this rare plant.

The most common way to test for pollination limitation is through experimental cross pollinations (e.g., Lee and Bazzaz 1982, Stephenson 1984, Garwood and Horvitz 1985). If fertilizations are limiting, the number of viable seeds produced in hand pollinated fruit should be higher than in insect pollinated fruit. A higher percentage of fruits should develop from hand pollinated flowers (less fruit abortion) if pollen is a limiting resource.

Resource limitation may be tested in a variety of ways. Adding water and/or nutrients tests whether resources limit plant size (Lee and Bazzaz 1982), plant survival (Grieg-Smith and Sagar 1981), fruit production (Lloyd 1980, Willson and Price 1980, Stephenson 1981, Stephenson 1984, Lee and Bazzaz 1982, Gorchov 1988) or seed production (Willson and Price 1980, Stephenson 1984; Gorchov 1988). Others have tested resource limitation of fruit and seed set through defoliation (Willson and Price 1980, Stephenson 1981, Stephenson 1984, Gorchov 1988), shading (Willson and Price 1980, Stephenson 1981), fruit thinning (Lloyd 1980, Gorchov 1988), girdling (Stephenson 1981, Gorchov 1988) and removal of competitors (Greig-Smith and Sagar 1981).

In this study I conducted one type of manipulation, resource addition, to test for resource limitation. Plants receiving extra water and/or nutrients should have more resources to mature viable seed if reproduction is limited by resources (Lee and Bazazz 1982, Stephenson 1984).

Study Area and Plant Description

Sidalcea malvaeflora ssp. *elegans* occurs from southern Douglas County through Curry and Josephine Counties in southwestern Oregon to Del Norte County in northeastern California. Eighteen small, localized populations are documented from throughout this range. The study area, Oak Flat, is near the confluence of the Rogue and Illinois Rivers in Siskiyou National Forest, southwestern Oregon. The dominant overstory consists of *Quercus garryana* and *Q. kelloggii*; the understory is mostly a mixture of introduced annual grasses.

This subspecies is distinct in that it is the only clonally-growing member of the *Sidalcea malvaeflora* group. Clonal mats range in area from 1 to 8 m^2 and, in the study population, are spatially segregated into 7 patches of plants. Patches produced from 1 to 31 racemes in 1988. Because of the clonal nature of this plant, it is difficult to determine how many racemes each plant erects. In the following experiments, I assume that racemes act independently of one another. There is a possibility, however, that manipulation of one raceme will affect the next because interconnected shoots may compete for and/or share resources. Racemes emerge in early April and flowering occurs throughout June. These plants are obligate outcrossers; self-pollinated plants produced no seed (pers. obs.).

Methods

Non-Experimental Data

In 1987 and 1988 I made systematic, non-experimental observations, the purpose of which were to gather baseline data on reproductive biology. These data were used to monitor predation, floral abortion rates and numbers of viable seeds produced by single and multi-fruited racemes. Baseline data collected in 1988 were also used as controls for 1988 experiments.

I marked 100 racemes each year using numbered wooden stakes and recorded number of buds per plant, flowers reaching anthesis (1988 only), fruits initiated (1988 only), and fruits matured each week from April-July. In 1987 2 plant markers were lost because of anthropogenic disturbance, making the total racemes monitored 98. Racemes were collected and dried. Fates of ovules were categorized as: missing (dispersed, viability unknown), aborted and/or undeveloped, attacked (presumably by the weevil *Macrorhoptus niger*) and viable. Viability was determined through germination tests in which seeds were placed in petri dishes to allow imbibition, scarified with a sterile knife and allowed to germinate. The resulting seedlings were grown and donated to the local botanic garden.

Predation was analyzed to determine whether single or multi-fruited racemes were preferentially attacked by weevils. A Chi-square test was used to analyze whether there was a difference in the number of ovules attacked per raceme on single and multi-fruited racemes. All racemes from the baseline population which did not have dispersed ovules were used for this analysis.

Experimental Data

Pollination Limitation

Experimental pollinations were conducted in 1988 to test whether seed production in *Sidalcea malvaeflora* ssp. *elegans* is pollinator limited. I randomly selected ten racemes with a total of 33 flowers. If stigmas were extended on my weekly visit, I cross-pollinated the flower using a small paintbrush and pollen from another clone (patch). Racemes were bagged when not being hand pollinated to discourage weevil infestation and to recover all ovules. I collected and dried racemes and categorized ovules as above.

A Chi-square test was used to analyze whether there was a difference in the proportion of hand and open pollinated fruit bearing viable seed. Controls were all racemes in the baseline population which experienced no seed predation (comparable to bagged racemes) and which had no dispersed seeds (so that the fates of all seeds were known).

Resource Limitation

Water and/or nutrients were added to 30x30 cm plots to determine if additional resources would increase viable seed production. Placement of plots was biased; they were set up in areas where plants grew vegetatively during the beginning of the field season. On average 0.5 racemes were produced per plot (range 0-2). There were seven replicates of each of the four following plot treatments: (1) control (no addition), (2) water (1 liter per week), (3) a one-time nutrient addition (19 g fertilizer, time-released 14% N/14% P/14% K per plot), and (4) water + nutrient (initial fertilizer plus 1 liter water per week). All treated racemes were collected, fruits were dried, and ovules categorized.

Results

Non-Experimental Data

Baseline information on production of reproductive parts was obtained from 98 racemes in 1987 and 100 racemes in 1988: number of buds per raceme averaged 4.62 (range 1-12), number of flowers averaged 3.70 (range 1-10), and number of fruits averaged 1.55 (range 0-7). The number of ovules per fruit was the most constant, averaging 6.0 (range 4-9).

Predation by the weevil, *Macrorhoptus niger*, and nondevelopment were the most common fates of ovules at Oak Flat in 1987 and 1988 (Table 1). It was clear that most of the seed destruction was due to the weevil because adult beetle pairs were found in *Sidalcea* flowers and larval and pupated forms were found in dried fruits during ovule analysis. Numbers of dispersed seeds were similar in both years. When rainfall was greater during fruit and seed maturation (1988), viable seed set doubled.

The pattern of weevil predation was analyzed to determine whether weevils preferentially attacked racemes with more fruits. The number of attacked ovules per raceme from 21 single-fruited racemes (62 flowers, 35 attacked/120 total ovules) was compared to the number of attacked ovules per 27 multi-fruited racemes (113 flowers, 65 fruits and 144 attacked/383 total ovules). Multi-fruited racemes experienced a much higher attack rate ($\chi^2_{1df} = 42.5$, $p < .005$). However, when predation rate was analyzed per fruit (number of attacked ovules per fruit), there was no difference in ovular attack rate in single and multi-fruited racemes ($\chi^2_{1df} = 2.33$ n.s.).

The pattern of abortion on floral parts from bud to mature fruit was examined on the baseline populations in both 1987 and 1988. Only about 10 percent of racemes matured all fruits they initiated (12.2% in 1987 and 9.0% in 1988), while nearly 30 percent aborted all fruits (34.7% in 1987 and 30.0% in 1988). In 1988 abortion rates between stages were more thoroughly monitored to determine at which stage(s) abortion took place; between bud and anthesis 19.9 percent of buds were aborted, between flowering and fruit initiation 50.6 percent were aborted, and between fruit initiation and maturation abortion was 15.4 percent.

Pollination

The ten racemes that were hand pollinated produced thirty-three flowers. Only eighteen flowers were receptive to pollination during my visits; seven fruits and 12 viable seeds out of 39 total ovules matured. Twenty-three unmanipulated open pollinated racemes, serving as the control group, produced 36 fruits, 73 flowers and 32 viable seeds out of 207 total ovules. There was a difference in the number of viable seeds produced per fruit in hand and open pollinated fruit ($\chi^2_{1df} = 3.91$, $p < 0.050$).

Resource Limitation

In Oak Flat *Sidalcea* in 1987 I compared single and multi-fruited racemes of 100 baseline plants and found that 70% of the viable seeds produced were from single-fruited racemes (of the 62 racemes which produced fruit, 32 were single-fruited). In 1988, the 100 baseline single-fruited and multi-fruited racemes produced roughly proportional numbers of viable seed; 24 single fruited racemes (34% of total racemes) produced 36.0 percent of total viable seeds while 46 multi-fruited racemes (66% of total racemes) produced 64.0 percent of total viable seeds.

The purpose of resource additions was to partition effects of water and/or nutrient limitation on viable seed set. The results may be compared but the sample sizes are small, and thus too variable, to detect any statistical differences. Water appears

TABLE 1. Percentages of ovules collected from control racemes in 1987 (98 racemes) and 1988 (100 racemes).

	Viable* (%)	Undeveloped** (%)	Missing (%)	Attacked (%)	Total Ovules	Total Flowers	Matured Fruit
1987	3.3	41.1	16.9	38.7	302	–	105
1988	7.1	51.5	15.1	26.3	930	370	155

*Ovules were deemed viable if they germinated after laboratory treatment.

**Includes aborted and unfertilized seeds.

TABLE 2. Fate of ovules in fruit receiving additional water and/or nutrients as compared to fruit from the natural environment.

Treatment	Total Racemes	Total Fruit	Total Seeds	Viable Seed/ Fruit	Ovules Eaten/ Fruit	Ovules Undeveloped/ Fruit
Water	2	5	29	2.00	1.40	2.40
Nutrient	3	4	21	0.00	2.75	2.50
Water/Nutrient	2	5	30	0.60	1.40	4.00
Control	100	155	931	0.43	1.58	4.00

to be a limiting factor; fruits receiving extra water produced over four times the number of viable seeds per fruit than controls (Table 2). The effect of additional nutrients may decrease viable seed set because no viable seeds were produced.

Discussion

In both 1987 and 1988 viable seed set in *Sidalcea malvaeflora* ssp. *elegans* was very low (3.3% and 7.1% of the total number of ovules respectively). Some of the missing seeds may have been viable; the actual seed set may have been higher. Arnold (1982) cites low seed sets for other self-incompatible perennials: *Dicentra canadensis* (2-7%), *Erythronium albidum* (6-11%) and *Linaria vulgaris* (1.4%).

There are two levels on which this population of plants seems to be producing, and subsequently aborting, floral parts. The first is a common overproduction of floral structures (buds, flowers, fruits) that may be caused by genetic or developmental abnormalities or by a response to limited resources (Stephenson 1981). Some abortion occurred between bud and anthesis (19.9%) and between fruit initiation and maturation (15.4%), but the bulk of floral structure loss took place between flowering and fruit initiation (50.6%). The high incidence of floral abortion between anthesis and fruit initiation may be seen as an adaptation either to respond to environmental stress or to eliminate fruits containing many aborted or unfertilized ovules (Udovic and Aker 1981).

The second level on which *Sidalcea* is producing and aborting floral parts is ovular. Harper (1977), Lloyd (1980) and Stephenson (1981) suggest some type of internal regulation is responsible for this abortion and Salisbury (1942) suggests "internal competition," both of which imply resource limitation. Gorchov (1988) points out that unfertilized ovules and fertilized ovules that subsequently abort must be distinguished because the first type of abortion is primarily determined by lack of fertilization and the latter may be determined by lack of resources. The large proportion of undeveloped (unfertilized and aborted seeds lumped together) seeds in this *Sidalcea*, 41.1 percent in 1987 and 51.5 percent in 1988, suggests that seed initiation may be limited by the pollination system. In 1988 mean viable seed production per fruit in *Sidalcea* was higher in hand extraclonally pollinated fruit than insect pollinated fruit (1.71 vs. 0.89). Two explanations for the lack of development might be that the system is limited by the number of pollinators or, more plausibly, much of the pollen received by flowers from insects is intraclonal and thus incompatible. Although seed set was higher in hand pollinated racemes, fruit set was not. Thus, pollination limitation may affect the distribution of seeds among fruits but not total fruit set.

Seed predation caused the second greatest limitation of seed set. Seeds of this plant experienced high predation from the weevil, *Macrorhoptus niger*, as evidenced by its presence in all its developmental forms within *Sidalcea* flowers and fruits. Predation rates such as those seen in *Sidalcea*, 38.7 percent and 26.5 percent, are not uncommon. Lee and Bazzaz (1982) cite a range of 0-49 percent of seeds attacked by weevil larvae in *Cassia fasciculata*. Multi-fruited racemes were preferentially attacked by weevils (5.33 seeds/raceme vs. 1.67 seeds/raceme on single-fruited racemes), but predation was not significantly different per fruit (2.21 seeds/fruit vs. 1.67 seeds/fruit on single-fruited racemes). Even though a clone which spreads out its fruit in several single-fruited racemes might escape predation (per raceme) better than a clone which produces a single multi-fruited raceme, the production of more fruits for weevils to choose from on multi-fruited racemes seems to negate any advantage in escaping predation single-fruited racemes might have.

Preliminary evidence suggests that resources also limit viable seed set. Single-fruited racemes from the baseline population produced more viable seed than multi-fruited racemes during 1987, but when more water was available, viable seed set was roughly equal. Gorchov (1988) found that treatments that reduced the number of plant parts competing for resources produced higher fruit sets than controls.

Although I attempted to partition the suggested resource limitation into water and/or mineral nutrients, both predation and small sample sizes complicate interpretation of results. However, the fact that racemes receiving extra water produced more viable seeds than controls suggests that water may be a limiting factor.

In Oak Flat *Sidalcea,* three factors seem to be acting to limit seed set: lack of pollination, limited water and seed predation. Because this species is rhizomatous, plants may spread throughout current habitats through asexual reproduction. However, seed production is necessary for establishment of new populations. Because established populations may persist indefinitely through clonal growth, I suggest simply monitoring the density of emergent leaf clumps per meter squared in clonal patches of selected populations to determine whether population size is increasing or decreasing. If population sizes decline, I suggest a combination of three management strategies to increase seed set: cross pollinations, water additions and/or predator exclusion.

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Clonal Propagation of Meadowfoam (*Limnanthes* sp.) from Bisected Seeds

Abstract

A method was developed to select and propagate meadowfoam lines that produce seeds with high oil content. Seeds of a meadowfoam hybrid (*Limnanthes* sp., ORL 85-765) were bisected so that a portion of the seed could be analyzed for oil content. The remainder of the seed was then germinated. Higher germination rates and more uniform plants were obtained from seeds cut transversely than from seeds cut longitudinally. Half seeds were stored frozen for 25 days without decrease in viability. Sterile plants were established by culture of shoot meristems taken from greenhouse-grown plants. Plants in sterile culture were cloned by micropropagation. This method of selection is more specific to genotype than sampling seeds from a population, and is easier than selection from tissue culture, because the half-seed method does not require sterile technique.

Introduction

Meadowfoam (*Limnanthes* sp.) is a short-lived annual with potential as a new oil seed crop (Jolliff 1981, Reed 1991, Southworth and Kwiatkowski 1991). Agronomists are working to increase oil yield by improved cultivation methods and by selection of seeds with high oil content for use as parents (Jolliff 1981). Analysis of individual seeds for oil content in the search for superior oil producers requires sacrifice of a portion of the seed for analysis. What is needed is the ability to identify oil-rich seeds and then to germinate them. If a portion of the seed could be analyzed and the remainder stored and later cloned, selection of high oil-producing parents would be greatly simplified. A half-seed technique has been used for analysis and subsequent germination in such genera as *Cucurbita* (Gathman and Bemis 1981) and *Brassica* (Pleins and Friedt 1989). This investigation addresses the feasibility of bisected seed storage, germination and clonal propagation of meadowfoam.

Methods and Materials

Seeds of *Limnanthes* sp. seed line ORL 85-765 selected from hybrids of *L. floccosa* ssp. *grandiflora* Arroyo X *L. alba* Hartw. in Benth. were obtained from Dr. Gary Jolliff, Department of Crop Science, Oregon State University. A plant variety protection application is pending.

Bisection of Seeds

Establishment of meadowfoam plants was compared for the following treatments: (a) whole seeds; (b) longitudinally bisected dry seeds; (c) longitudinally bisected seeds that had been pre-imbibed at 10°C before bisection; (d) transversely bisected dry seeds; and (e) transversely bisected dry seeds which were stored at −14°C for 25 d following bisection. For treatments (a)-(d), 30 seeds were cut and divided into three Petri dishes for germination. For frozen storage, 32 seeds were cut, stored frozen, and divided into four dishes for germination.

Results were analyzed by a chi-square contingency table to determine the significance of deviations from the pooled estimate of germination (Samuels 1989).

"Seed coats" in *Limnanthes* consist of a testa-pericarp with the fruit wall adhering to seed coat and embryo in both dry and imbibed conditions. In preliminary experiments, the testa-pericarp was chipped off with a scalpel, but this process was laborious and potentially damaging to the embryo. We proceeded without removing the testa-pericarp. Seeds were sliced longitudinally or transversely through the center by holding them with curved forceps on a hard surface, and slicing with a number 10 blade fitted scalpel. Longitudinal cuts, (b) and (c), were made through the long axis of the seed. The position of the cotyledons in relation to the longitudinal cut was not determined, as no obvious external marks on the seed indicated cotyledon position. Some longitudinal cuts separated the cotyledons; others cut both cotyledons lengthwise. Frequently the embryonic axis (radicle-hypocotyl-epicotyl) was cut. Transverse cuts, (d) and (e), were made across the seed, halfway between the basal attachment scar and the seed tip. This cut off the distal portion of both cotyledons, but did not cut the embryonic axis.

For the pre-imbibition treatment, seeds were hydrated on filter paper moistened with distilled water at 10°C in the dark for 40 h prior to bisection. For frozen storage at −14°C, seeds were transversely bisected, placed in a 96-well polystyrene microtitre plate and sealed with parafilm.

Seed Germination

Seeds from all treatments were imbibed on moist filter paper in sealed Petri dishes at 10°C in darkness for 9 d, after which they were planted in flats of soil by placing the emerging radicle, when present, in the downward position, and barely covering the seeds with potting soil. Sterile technique was not used as a test of the utility of the method to growers. Flats were placed in a greenhouse under a 10-11 h photoperiod in October and November in Ashland, OR, with temperatures of 22°C day and 15°C night, and watered daily. No fertilizer was applied.

After 12 d in the greenhouse, plants were counted as established if one or more true leaves had formed. Results were analyzed by a chi-square contingency table with the expected rate of plant establishment determined from the pooled estimate.

Meristem Culture

After an additional 28 d in the greenhouse, when plants were maturing, but not flowering, apical meristems were aseptically excised and cultured on a liquid medium consisting of MS salts, vitamins (Nitsch and Nitsch 1969), indoleacetic acid (IAA, 0.1 mg/1), gibberellic acid (GA, 0.2 mg/l), kinetin (0.04 mg/l), and sucrose (30 g/l). The pH was adjusted to 5.6 with NaOH. Medium was dispensed, 10 ml per tube, into 20 x 150 mm culture tubes with polypropylene caps and autoclaved for 12 min at 110°C (Brown and Kwiatkowski 1988). After 10 d culture on liquid media, meristems were subcultured to semi-solid media containing carbenicillin (250 mg/l) for control of a slow-growing bacterial contaminant.

Cytokinins were tested to determine which best promoted shoot multiplication. The test material consisted of shoot clumps of *L. alba* var Foamore derived from somatic embryos grown on the above MS medium without plant growth regulators, except trans-zeatin (0.2 mg/l) and with agar (6 g/l) (Southworth and Kwiatkowsi 1991). Under a laminar flow hood, clumps were dissected to single shoots and transferred, three shoots per 250-ml flask, to the same medium containing N^6-benzyladenine (BA), trans-zeatin, kinetin, or N^6-($\triangle^2$-isopentenyl)-adenine (2iP), all at concentrations of 1 mg/1. Flasks were placed in the growth chamber under 8-h d (19 $\mu Em^{-2}s^{-1}$) and 18°C/12°C day/night temperature regime. After 43 d when shoot clumps were mature and senescence was beginning, clumps were dissected to count the number of shoots.

Data were subjected to one-way analysis of variance (ANOVA) to test whether sample means were drawn from populations with the same mean (Samuels 1989).

Plant material from one flask of each treatment was subcultured to semi-solid (6 g/l agar) modified MS media containing IAA, GA, and kinetin, as above (Brown and Kwiatkowski 1988), for rooting and then transplanted to soil in the greenhouse.

For shoot multiplication, plants derived from meristem culture of *Limnanthes* sp. (ORL 85-765) were placed on 50 ml semi-solid MS media containing trans-zeatin (1 mg/1) and carbenicillin in 250 ml flasks plugged with cotton. Flasks were placed in the growth chamber as above.

Results

All treatments yielded high germination percentages (Table 1). After incubation of seeds for 8 d, radicle emergence was least for longitudinally bisected dry seeds in which 73 percent of seeds produced radicles. In all other treatments, at least 97 percent of seeds produced radicles. Based on chi-square analysis, germination percentages differed significantly from the pooled estimate of germination which was 0.93.

The manner of cutting affected plant growth. The number of plants established in the greenhouse after 8 d incubation at 10°C and 12 d in the greenhouse was greatest for transversely bisected dry seeds of which 100 percent gave rise to plants. Plant establishment was least for pre-imbibed, longitudinally bisected seeds in which 77 percent of the seeds yielded plants (Table 1). Of transversely bisected frozen seeds, 97 percent formed plants. In some dry seeds, cotyledons shattered or cracked when bisected while pre-imbibed seeds did not shatter or crack, but cut smoothly. However, a larger fraction of seeds that were cut dry gave rise to plants (Table 1). Some seeds with emergent radicles after the cold treatment failed

TABLE 1. Effect of cuts on radicle emergence and establishment of plants.

Treatment	Emergence of Radicles[1]		Establishment of Plants[2]	
	Germ.	Ungerm.	Growth	No Growth
Whole seed	29	1	28	2
Longitudinal bisect	22	8	26	4
Imbibe, longi-bisect	30	0	23	7
Transverse bisect	29	1	30	0
Trans-bisect, freeze	31	1	31	1
Chi-square value	21.39		12.48	

[1]Radicle emergence 8 d after imbibition; $p < 0.0001$.
[2]Determined 12 d after planting; $0.001 < p < 0.01$.

to develop into plants, and some seeds lacking emergent radicles eventually grew.

After 12 d in the greenhouse, seedlings from whole seeds showed the greatest vigor, being larger than those from all other treatments. Seedlings from pre-imbibed seeds were the smallest. Seedlings from the dry, transversely bisected seeds, whether germinated immediately or stored, and the dry longitudinally bisected seeds had similar intermediate vigor, but the longitudinally bisected seeds showed more variability. They had both larger and smaller seedlings than the transversely bisected seeds in which seedlings were more uniform. These differences in seedling size continued. After 43 d in the greenhouse, plants from whole seeds were larger than those from all other treatments, and had many flower buds. Plants from bisected seeds were smaller, and had fewer flower buds.

Meristems from ORL 85-765 grew rapidly, although 25 percent were lost due to contamination. Meristems grew from an excised length of 0.3-1.0 mm to lengths of 3-15 mm in 9 d. Subculture to semi-solid media from liquid media was necessary after 10 d. After an additional 55 d on media with zeatin (1 mg/l) and carbenicillin, seven out of ten shoots survived and produced an average of 7 ± 3.1 shoots per clump.

Shoot multiplication of meadowfoam also occurred on media containing zeatin, kinetin, or 2iP, but not on media containing BA. Multiplication was best on zeatin (Table 2), but kinetin and 2iP gave satisfactory results. Differences in treatments were significant ($F = 29.11$, d.f. 3, 32, $P < 0.0001$). Based on the Newman-Keuls procedure, the means of numbers of shoots developed on zeatin and on BA differed from those of all other cytokinins at the 1% level (Samuels 1989). Meristems treated with kinetin did not differ significantly from those treated with 2iP.

TABLE 2. Shoot multiplication in response to cytokinins in *L. alba* var. Foamore.

Cytokinin (1 mg/l)	Shoots per Clump[1]	
	$\bar{X}$	SE
Zeatin	9.8	0.9
Kinetin	6.7	0.4
N^6-($\triangle^2$-isopentenyl)-adenine	6.7	0.9
N^6-benzyladenine	1.0	0

[1]43 d in culture; n = 9.

Discussion

Transversely bisected seed was easier to work with than longitudinally bisected seed. Plants grown from transversely bisected seeds were more uniform, and germination and growth were more reliable. With longitudinally bisected seeds, it was difficult to determine which half would be viable, as both halves may have contained some apical tissues. We observed that only one half formed a plant. Longitudinally bisected seed consisted of proportional amounts of testa-pericarp and cotyledonary tissues, and in addition, apical tissues in varying amounts. Transversely bisected seed provided a more uniform tissue for analyses, because the decapitated portion consisted only of proportional amounts of testa-pericarp and cotyledonary tissues.

These results show that a rather crude cut under non-sterile conditions yields a half seed that can be stored frozen while the other half is analyzed for oil.

While *Limnanthes* sp. grows well in tissue culture, this method requires relatively high technology with sterile conditions (Reed 1991, Southworth and Kwiatkowski 1991). Establishment of *Limnanthes* sp. embryos in culture occurred with the loss of a high percentage of embryos due to handling damage or contamination (Southworth and Kwiatkowski 1991). The half-seed method applies appropriate technology to develop a useful selection procedure.

The rapid growth of plants from meristems indicates that meadowfoam is well suited to meristem

culture. Refinements in meristem excision should overcome contamination, as the meristem itself appeared to be free of microorganisms. When excising apical meristems, it was noted that most leaf petiole bases were contaminated with soil particles. Only the innermost six to eight leaf bases surrounding the meristem were reliably free of soil particles. This level of surface contamination so deep within the rosette indicated difficulty in surface sterilization for shoot culture, as noted by Reed (1991). Meristem culture should overcome leaf axil contamination, as the innermost primordia seemed to be clean.

Failure to obtain shoot multiplication on BA differed from the results of Reed (1991) who used BA as the sole cytokinin and obtained 2.4 shoots per clump. The differing outcomes may be due to genetic differences in selected lines, to developmental differences induced by previous culture conditions such as growth on zeatin, or to environmental differences such as warmer days.

The ability to store bisected seeds and later to regenerate and clonally increase plants from those half seeds should enhance the effort to breed a superior oil-producing meadowfoam.

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Pacific Northwest Forest Lands Potential for Floral Greenery Production

Abstract

This study was undertaken to determine the management potential of forest plant zones in the Pacific Northwest for floral greenery production. The special forest products industry, based primarily on the utilization of understory plants found in Northwest forests, employs thousands of part-time and full-time people. To date, little information has been published concerning the special forest products industry (Schlosser *et al.* 1991). This paper describes the forest zones and selected plant associations of the region which have the greatest potential for floral greens management.

Plant association guides completed by the U.S. Forest Service and other research groups have been used to identify specific forest associations across five forest zones in the region. The occurrence, in terms of constancy and coverage, of each species in a number of these associations is given. Harvest levels of each product are discussed while specific associations are recommended for floral greens management.

The special forest products industry leases harvest rights from forest landowners. The leases typically generate annual revenues which can continue during the entire life of the forest stand. The increasing importance of generating revenues from Northwest forests places increased emphasis on the proper management of floral greens for harvest.

Introduction

The coniferous forests common to western Washington, western Oregon, and coastal British Columbia contain sites rich in understory vegetation. Many understory plants of this region have characteristics desired by the floral greens industry. Forest plants have been harvested from Northwest forests over the past fifty years by a group of businesses known as the special forest products industry. The portion of the industry dealing with understory plants is known as the floral greens industry, with individual buyers/processors referred to as producers.

Most plant parts purchased by floral greens producers are used to accent floral arrangements and provide long lasting backings and fillers for colorful flowers. Waxy leaved evergreen plants, such as salal (*Gaultheria shallon*)[2] and evergreen huckleberry (*Vaccinium ovatum*) are harvested, processed, and marketed extensively. Plants with similar properties, such as dwarf Oregon-grape (*Berberis nervosa*) are also in high demand as floral greens. Sword fern (*Polystichum munitum*) and deer fern (*Blechnum spicant*) are desired for their flexible fronds and unique form. Beargrass (*Xerophyllum tenax*) is harvested, dried and dyed for use in eastern United States and European floral markets. These and other plants are common to several forest associations found across the Pacific Northwest.

The special forest products industry also purchases a wide array of other plant materials such as cones, evergreen boughs, mushrooms, and mosses. In 1989, the special forest products industry generated an estimated $47.7 million in raw product purchases for an estimated $128.5 million in finished product sales and employed over 10,000 persons in seasonal and permanent positions (Schlosser *et al.* 1991).

The special forest products industry is concentrated in western Oregon, western Washington, and southwestern British Columbia. Many of these businesses extend their procurement efforts hundreds of miles. Forest landowners of the region have the opportunity to enter into harvest lease agreements with the producers and harvesters of the products. The harvesting process typically removes only a portion of the plant, and allows for harvest annually or in alternate years.

Many public and private forest managers are becoming more interested in special forest products because of the revenue potential associated with the sale of harvest leases. As a result, methods are being sought to manage for the production of special forest products in combination with other more traditional forest outputs. Public land managers in the U.S. Forest Service, the Washington State Department of Natural Resources and the Oregon Department of Forestry have recognized the monetary potential associated with leasing harvest rights to special forest products producers. Additionally, numerous private forest landowners (industrial and nonindustrial) have offered special forest product harvest leases.

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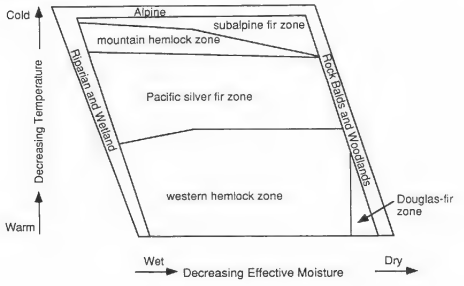
[2]All scientific and most common names are defined according to "Flora of the Pacific Northwest" (Hitchcock and Cronquist 1981). Some common names used may reflect specialized usage by the floral greens industry.

This paper provides a preliminary assessment of the potential for producing selected floral greens within the subalpine fir, mountain hemlock, Pacific silver fir, western hemlock and Douglas-fir forest zones. Management options are also discussed for the joint production of the floral greens and other forest uses.

Methodology

Plant association guides have been completed for most of the forested part of the Pacific Northwest by the U.S. Forest Service and others. These guides present the characteristics of forest associations with discussions of management, soils, microsites, and species composition. The guides were used in this study to identify forest associations supporting species desired by floral greens buyers.

Forest communities from each geographic area represented in the guides were arrayed by forest zone. The classification of western Washington, western Oregon and coastal British Columbia into forest zones generally appears in the ecological literature as a two-dimensional aggregate reflecting a temperature regime and a moisture gradient (Topik *et al.* 1988, Halverson *et al.* 1986, Brockway *et al.* 1983) (Figure 1). The moisture and temperature axes are arranged to reflect elevation and aspect-related climatic information. To facilitate information processing, the zones were ordered in a linear fashion. The ordering represented a moisture/temperature gradient which moved from cold/wet at one extreme, to warm/dry at the other extreme.



Linearized ordering of the forest zones from the moisture/temperature distribution:

Cool-Wet				Warm-Dry
subalpine fir zone	mountain hemlock zone	Pacific silver fir zone	western hemlock zone	Douglas-fir zone

Figure 1. Idealized distribution of forest zones within a temperature and moisture gradient, adapted from Topik *et al.* (1986) and Halverson *et al.* (1986).

In each zone, plant associations were ordered and recorded using the same linear criteria used for ordering the zones. For example, the western-hemlock zone supports numerous plant associations. On the Gifford Pinchot National Forest, western hemlock communities tend to exist in the geographic areas exhibiting the combinations of moisture and temperature evidenced in Figure 2 (Halverson *et al.* 1986, Topik *et al.* 1986). From this idealized two-dimensional distribution, specific associations were grouped in the general temperature/moisture combinations shown in Table 2. From these general groups, associations were ordered from cold/wet to warm/dry extremes.

Many plant associations are found throughout the region. Because of subtle differences in the floristic composition of various national forests and study areas, not all plant associations represented in one forest are represented in another forest. In cases where specific plant associations were not represented in each national forest, the association was ordered according to the temperature/moisture gradient in the forest zone in which it occurred.

Plant association guides present tables of individual plant constancy and coverage values for each forest association. Constancy, expressed as a whole number percent, represents the presence of a plant species within an association with no emphasis on either size or numbers (Kovalchik 1987). Coverage denotes the average percentage, expressed as a whole number, of canopy coverage for each plant species within a plant association (Clausnitzer and Zamora 1987). Eight of the most economically important floral greenery species were identified in a survey of special forest products producers (Table 2) (Schlosser *et al.* 1991). By recording the constancy and coverage values for each of the floral greens species by forest association, a summary of the relative degree of plant coverage and occurrence was obtained.

Plant association guides also discuss microclimate, floristic successional stages, soil characteristics, animal use and management considerations by plant association. By synthesizing this information, management concerns are highlighted to aid in the identification of lands with the potential for joint production of special forest products and other forest uses.

Background

General Product Quality Considerations

The ecological requirements of the floral greens are as diverse as the habitats in which they grow.

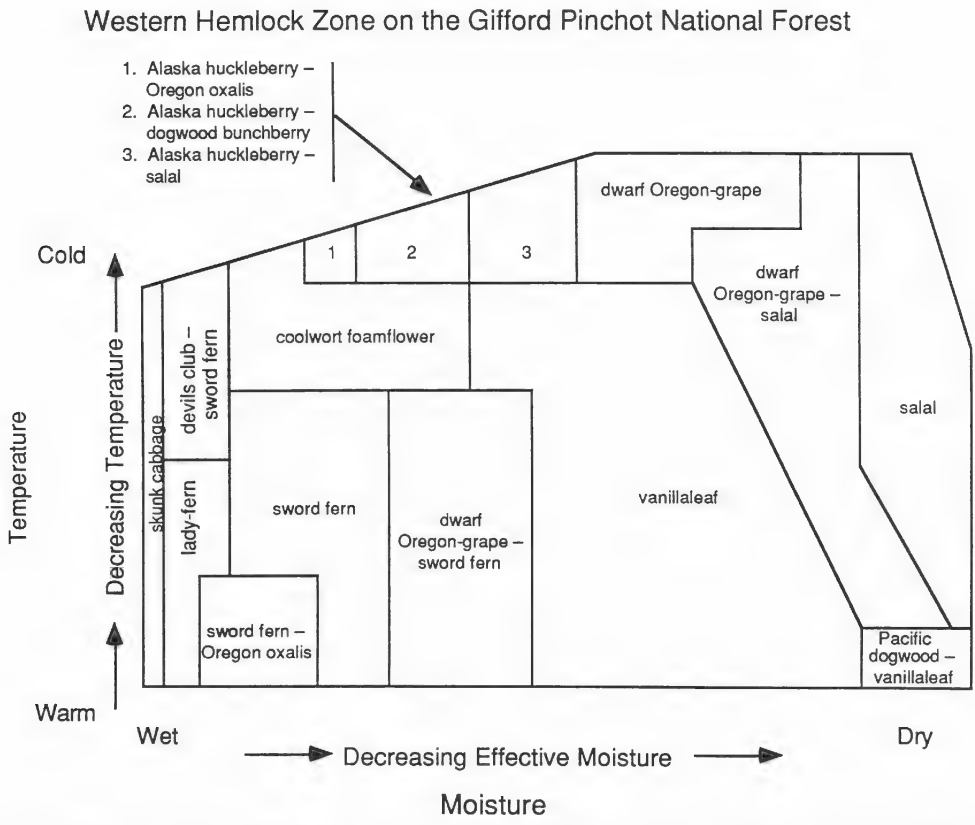


Figure 2. Predominant understory plant locations as evidenced by a temperature and moisture gradient common in the western hemlock zone. See Table 2 for general groupings of these associations and scientific names. Adapted from Topik *et al.* (1986) and Halverson *et al.* (1986).

Most of the floral greens species require partial shade provided by overstory forests to meet product quality requirements. Salal, evergreen huckleberry, dwarf Oregon-grape, deer fern, sword fern and Oregon-boxwood (*Pachistima myrsinites*) require a partially closed forest canopy to grow in forms acceptable for commercial harvest. Although most of these plants grow under other conditions, only plants growing under partial shade develop the deep green, broad spreading leaves or fronds desired by floral greens producers.

Forest site disturbances, such as fire and timber harvesting, often create early seral conditions favoring other floral greens species. Beargrass, grown in the open, produces long, bluish-green leaves which retain strength and color after harvest. Scotch broom (*Cytisus scoparius*), an introduced species, grows tall and straight in openings with deep green color. Red-evergreen huckleberry (*Vaccinium ovatum*)[3] grown in direct sunlight, develops long spikes with leaves arranged spirally along the stem. In direct sunlight these leaves turn bright red, thus giving it the alternate vernacular of "red-huck."

Salal appears in early successional stages on many sites but it is seldom of harvestable quality until it has developed under a partial canopy of

[3]Note evergreen huckleberry and red-evergreen huckleberry (red-huck) are both *Vaccinium ovatum*. The different common (trade) names reflect differences in plant coloring and are important in the floral greens trade. The red tips associated with *Vaccinium ovatum* grown in direct sunlight (red-huck) are marketed and used in different ways than *Vaccinium ovatum* grown under shade.

TABLE 1. Examples of the forest associations found in the western hemlock zone on the Gifford Pinchot National Forest.

PLANT ASSOCIATIONS WITHIN THE WESTERN HEMLOCK ZONE*			
WET GROUP	MOIST GROUP	MESIC GROUP	DRY GROUP
skunk cabbage *Lysichitum americanum* lady-fern *Athyrium filix-femina* devils club *Oplopanax horridum*- sword fern *Polystichum munitum*	sword fern *Polystichum munitum*- Oregon oxalis *Oxalis oregana* Alaska huckleberry *Vaccinium alaskaense*- Oregon oxalis *Oxalis oregana* coolwort foamflower *Tiarella trifoliata* sword fern *Polystichum munitum*	dwarf Oregon-grape *Berberis nervosa*- sword fern *Polystichum munitum* Alaska huckleberry *Vaccinium alaskaense*- dogwood bunchberry *Cornus canadensis* Alaska huckleberry *Vaccinium alaskaense*- salal *Gaultheria shallon* vanillaleaf *Achlys triphylla* dwarf Oregon-grape *Berberis nervosa* dwarf Oregon-grape *Berberis nervosa*- salal *Gaultheria shallon*	salal *Gaultheria shallon* Pacific dogwood *Cornus nuttallii*- vanillaleaf *Achlys triphylla*

*Adapted from *Plant Association and Management Guide for the Western Hamlock Zone* (Topik *et al.* 1986).

TABLE 2. Common and scientific names of the species most widely utilized as floral greens.

COMMON NAME	SCIENTIFIC NAME
dwarf Oregon-grape	*Berberis nervosa* Pursh
deer fern	*Blechnum spicant* (L.) Roth
scotch broom	*Cytisus scoparius* (L.) Link
salal	*Gaultheria shallon* Pursh
Oregon-boxwood	*Pachistima myrsinites* (Pursh) Raf.
sword fern	*Polystichum munitum* (Kaulf.) Presl
evergreen huckleberry	*Vaccinium ovatum* Pursh
beargrass	*Xerophyllum tenax* (Pursh) Nutt.

trees. Salal products grow best under partial shade, but growth and vigor increases as canopy shading approaches complete closure (Sabhasri 1961, Haeussler and Coates 1986, Emmingham and Hanley 1986). Although sword fern, dwarf Oregon-grape, Oregon-boxwood and deer fern also grow in openings, these species require shaded environments to develop characteristics desired by floral greens producers. During the period from crown closure to forest maturity, these plants compete among themselves and with other plants. During this period the floral greens species meet product quality standards.

As forest communities mature, many understory plant species become scarce or totally absent. Depending on the forest zone, evergreen huckleberry and Oregon-boxwood generally have low representation in successionally advanced communities. Management practices to increase constancy and coverage of specific understory plants are best applied during early to mid stages of forest succession. By combining specific management practices for floral greens with the characteristics of specific forest associations, management practices may be used which allow for joint production of understory floral greens and other forest uses.

Forest Zones

A forest zone, as used here, represents areas in which the climate over time, favors the dominance of one forest tree species (Figure 1). The subalpine fir zone is found where cold conditions and

high elevations combine to produce short growing seasons. Where precipitation levels are slightly higher, usually in the form of deep snow packs, the mountain hemlock zone is prevalent. The Pacific silver fir zone predominates where precipitation levels are slightly higher than in the subalpine fir zone and the mountain hemlock zone, but temperatures are warmer usually due to lower elevations accompanied sometimes by south and/or west aspects. As growing seasons and temperatures increase, the western hemlock zone becomes predominant. As moisture availability decreases, the Douglas-fir zone is predominant, usually at lower elevations (Figure 1).

Results

Subalpine Fir Zone

A distinct subalpine fir zone has not been classified on all the national forests in the study region. This zone on the Olympic National Forest (Henderson *et al.* 1989) contains four recognizable subalpine fir associations. The area exhibits a continental climate with wide seasonal temperature extremes. The zone is used as summer range for big game. Late snow melt allows watershed management practices designed to increase delayed water yield. Soils in this zone are well drained and shallow while forest productivity is relatively low. Due to physical constraints and the remoteness of this zone, it is not well suited to intensive forest management.

Floral Greens Production Potential

Shrub and herb populations typically have low constancy and coverage values throughout the subalpine fir zone. The only harvestable floral greens plants present are beargrass, dwarf Oregon-grape and Oregon-boxwood. On the wet/cold sites, beargrass has constancy values ranging from 30 to 50 perent with coverage values ranging from 13 to 44 percent. Conversely, dwarf Oregon-grape has medium constancy values with only 1 percent coverage (Table 3).

Management Considerations

Management for floral greens harvest in this zone will most likely occur on associations which are exceptionally productive; average sites probably will not produce at levels necessary to sustain harvest at commercial levels. Where understory plant products exist, deer and elk often browse the new growth, reducing the quality of the product. Combining poor accessibility and dry location characteristics, intensive floral greenery management is not practical.

Mountain Hemlock Zone

The mountain hemlock zone is found at high elevations, with short growing seasons (Figure 1). It occurs at elevations above 1000 m (3300 feet) in areas receiving precipitation exceeding 2540 mm (100 inches) (Henderson and Peter 1985). Most of the precipitation falls as snow, usually accumulating snowpacks of about 3.3 m (10 feet) (Henderson *et al.* 1989, Henderson and Peter 1985). The biological productivity of this zone is very low due to excessively short growing seasons caused primarily by short frost-free periods (Henderson *et al.* 1989). The forest canopy is generally continuous but interspersed with small openings. This zone is a favorite of recreationists interested in panoramic views and of watershed managers interested in mid summer water flow. This zone is also important to big game management, as summer range for deer and elk.

Floral Greens Production Potential

Because of the short growing season of this zone, only a few floral greens species have suitable growth. Deer fern and beargrass are present on most sites. Beargrass typically grows on all sites except the wettest where devils club (*Oplopanax horridum*) predominates, or on the driest where rhododendron (*Rhododendron* spp.) predominates. Despite beargrass constancy values generally exceeding 50 percent, harvestable populations are scattered with coverage values between 2 and 65 percent (Table 3). Deer fern is not as tolerant of the cold-wet climates as beargrass, but it does occur in the Alaska huckleberry (*Vaccinium alaskaense*) association, becoming scarce in the rhododendron associations. Dwarf Oregon-grape and sword fern are present on some sites, but not in amounts needed for commercial harvesting.

Management Considerations

Due to the remoteness of this zone and its low timber productivity, much of the zone remains unroaded. In those areas which are roaded and where wildlife management is not adversely affected by

TABLE 3. Average coverage and constancy values for some floral greens plant species by selected forest associations [1] (Note: not all forest associations in the region are in this table).

Forest Association	AVERAGE COVERAGE/AVERAGE CONSTANCY[2]					
	dwarf Oregon-grape	deer fern	beargrass	salal	sword fern	evergreen huckleberry
Subalpine Fir Zone:						
Pacific rhododendron[3]	1/20	–	13/30	–	–	–
big huckleberry	–	–	44/50	–	–	–
Mountain Hemlock Zone:						
Alaska huckleberry	–	1/62	2/20	–	1/10	–
big huckleberry - Alaska huckleberry[4]	–	1/16	8/83	–	–	–
Alaska huckleberry - beargrass	–	2/50	15/100	–	–	–
big huckleberry	–	1/3	20/85	–	–	–
big huckleberry - beargrass	3/12	–	41/98	–	–	–
Pacific Silver Fir Zone:						
skunk cabbage	–	3/100	5/50	15/100	1/50	–
sword fern	3/65	7/94	1/62	3/50	21/100	–
salal - Oregon oxalis	12/85	5/100	4/42	19/100	5/85	–
Alaska huckleberry/Oregon oxalis	3/10	3/100	2/24	2/31	3/68	–
salal - deer fern	5/30	4/100	30/7	23/100	2/61	–
Western Hemlock Zone:						
vine maple/vanilllaleaf	25/100	–	–	2/8	9/100	–
Pacific dogwood/vine maple	22/100	8/5	2/10	17/13	4/73	–
salal	6/80	3/24	2/17	50/100	7/53	4/17
sword fern	4/74	2/45	1/7	3/47	37/100	3/50
sword fern - coolwort foamflower	7/63	3/60	–	3/71	39/100	5/26
dwarf Oregon-grape - sword fern	18/100	2/20	2/33	3/53	26/100	–
sword fern - salal	10/87	2/31	1/5	31/100	20/100	–
vine maple - salal	11/65	2/21	2/31	35/100	15/93	12/46
Pacific rhododendron - sword fern	7/89	2/32	1/23	22/55	22/82	5/56
Pacific rhododendron - dwarf Oregon-grape	15/100	1/11	2/31	4/66	10/70	7/75
Pacific rhododendron - salal	10/90	2/25	4/39	40/99	7/60	6/75
Pacific rhododendron	7/67	2/11	2/23	9/50	9/82	41/100
salal - evergreen huckleberry	3/100	–	–	68/100	4/100	9/100
evergreen huckleberry	6/43	2/39	–	9/87	43/100	21/100
salal - dwarf Oregon-grape	23/100	2/12	2/9	42/100	11/84	23/17
Douglas-fir Zone:						
salal	17/93	–	2/51	46/100	3/78	–
salal - oceanspray	19/100	–	2/31	35/100	2/85	–
oceanspray - dwarf Oregon-grape	26/100	–	–	3/25	2/78	–
oceanspray - baldhip rose	10/94	–	2/25	4/43	3/76	–

[1]Data for this table were derived from all of the plant association guides and other sources included in the references section of this paper.

[2]Values for constancy and coverage represent a simple average of all research areas classifying the specific plant association.

[3]Scientific names for the plant species representing the individual associations are presented in the text.

[4]A "/" is used to separate layers between species, while a "-" is used to separate species in the same layer. However, readers should be aware that the plant association guides for western Washington and western Oregon have not been standardized and hence some inconsistencies exist.

the increased use during the spring and summer months, beargrass may be commercially harvested.

Beargrass is generally found in stands of all ages. It resprouts quicker following fire than following disturbances from harvesting equipment (Henderson *et al.* 1989, Wright and Bailey 1982). Unfortunately, fire also accelerates Alaska huckleberry and big huckleberry (*Vaccinium membranaceum*) repopulation, which commonly excludes tree regeneration. As a result, the use of fire to increase harvestable beargrass populations should be avoided where deciduous huckleberry species are well-represented and tree regeneration is desired.

Pacific Silver Fir Zone

The Pacific silver fir zone occupies mid- and upper-slopes above 900 m (2970 ft.) in wet climates and 1480 m (4900 ft.) in the driest environments (Figure 1). Both winter temperature and snow fall are moderate with the snowpack melting by late-spring to mid-summer. Precipitation ranges from 2120 mm (80 in.) in drier areas to amounts above 5300 mm (200 in.) in wetter areas. This zone characteristically has cool, moist, shallow soils.

Floral Greens Production Potential

The Pacific silver fir zone is the cold extreme for many of the floral greens plant species. Constancy and coverage values are low for many, but not all floral greens species.

Dwarf Oregon-grape constancy values are highly variable ranging from 3 to 85 percent, with coverage values consistently below 10 percent. Dwarf Oregon-grape production is maximized in the cool-moist associations, but its constancy values remain moderate on sites which support warm-dry associations.

Deer fern is moderately well represented, as measured by constancy, on all but the driest sites. Values normally exceed 40 percent and exceed 90 percent in 5 associations (Pacific silver fir zone/: skunk cabbage (*Lysichitum americanum*); sword fern; salal - Oregon oxalis (*Oxalis oregana*)[4]; Alaska huckleberry / Oregon oxalis; and salal - deer fern associations) (Table 3). Although coverage values are generally near 5 percent, this value represents economically feasible harvest levels because of the dense, overlapping fronds of the plant. Deer fern population numbers decrease sharply on the warm-dry sites and is generally absent on extreme warm-dry locations.

Salal is well-represented across most of the environmental gradient present in the Pacific silver fir zone. In moist climates, where sword fern is predominant, it has constancy values up to 50 percent, with coverage values below 10 percent. At the drier extreme, salal also has very high constancy values with coverage values scattered between 3 and 35 percent. Salal typically requires only sporadic openings in the forest canopy to achieve highest product quality.

Sword fern is well suited to the moist and wet climates found in the Pacific silver fir zone. Where it is predominant, it has 100 percent constancy with up to 28 percent coverage. Like deer fern, sword fern has overlapping fronds and single plants are often spaced well apart. Thus, even low coverage values often signal acceptable harvest levels. In the drier-warm sites sword fern is less common and generally considered unharvestable for commercial purposes.

Beargrass is represented in almost all plant associations in the Pacific silver fir zone, but its highest potential for commercial utilization is found where it is either a dominant or co-dominant understory species. Where it attains this dominance it has constancy values between 85 and 100 percent with coverage values from 20 to 64 percent (e.g. Pacific silver fir zone/: Alaska huckleberry / beargrass; big huckleberry / beargrass; white rhododendron (*Rhododendron albiflorum*) / beargrass; Pacific rhododendron (*Rhododendron macrophyllum*) / beargrass; and beargrass associations). Beargrass is sporadically found at harvestable levels across other associations, such as the Pacific silver fir / salal - deer fern association on the Olympic National Forest, where coverage is 30 percent with a constancy of 7 percent (Henderson *et al.* 1989).

Management Considerations

Most of the Pacific silver fir zone is classified as ecologically fragile due primarily to soil characteristics (Henderson *et al.* 1989). Many regeneration prescriptions strongly recommend shelterwood regeneration techniques to maintain soil stability

[4]A "/" is used to separate layers between species, while a "-" is used to separate species in the same layer. However, readers should be aware that the plant association guides for western Washington and western Oregon have not been standardized and hence some inconsistencies exist. A ";" is used to separate the different associations within each example.

and soil nutrients while reducing erosion (Brockway *et al.* 1983). Forest management prescriptions designed to protect soil and organic matter are strongly recommended for this zone (Henderson *et al.* 1989).

On moist and wet sites (e.g. Pacific silver fir zone/: skunk cabbage; devils club; devils club - Alaska huckleberry; sword fern; and sword fern - Oregon oxalis associations), management practices such as shelterwood regeneration harvests with minimal disruptions to understory communities are complementary to deer fern, salal and sword fern populations.

On mesic to dry sites (e.g., Pacific silver fir zone/: white rhododendron; white rhododendron/ beargrass; Pacific rhododendron - Alaska huckleberry; Pacific rhododendron / dwarf Oregon-grape; Pacific rhododendron / salal; Pacific rhododendron; Pacific rhododendron / beargrass; and beargrass associations) commercial management for beargrass, salal and dwarf Oregon-grape is preferred. Although maintenance of organic matter is a concern on these sites, prescribed burning is acceptable (Brockway *et al.* 1983, Hemstrom *et al.* 1982). In shelterwoods with low residual basal area, salal competition tends to reduce tree regeneration. Where it is present in the association, salal will regenerate from roots, rhizomes and seeds stored deep in the forest floor, especially on drier sites (Feller 1988). Salal will not be of suitable quality for extended time periods following shelterwood regeneration treatments due to stunted growth from excess sunlight and droughty conditions (Sabhasri 1961). Where salal is the understory-dominant, burning is often used to control heavy concentrations of salal so that tree regeneration has a better chance of success (Brockway *et al.* 1983). Fire stimulates salal sprouting from roots and stem bases, but regrowth is slowed for five to ten years, compared with pre-burn levels (Haeussler and Coates 1986, Sabhasri 1961). Beargrass, dwarf Oregon-grape and sword fern tend to resprout following fire (Haeussler and Coates 1986), but only beargrass thrives and is harvestable in the open environment created. As forest trees grow to near crown closure, both salal and dwarf Oregon-grape become harvestable.

Western Hemlock Zone

The western hemlock zone has high floristic diversity and aesthetic appeal. It is characterized by precipitation levels less than 4000 mm (150 in.) but above 800 mm (30 in.), with brief summer droughts (Henderson *et al.* 1989). Most precipitation falls as rain, fog or cloud drip, with minimal snow accumulations. In wetter environments it occurs up to 300 m (1000 ft.) elevation, but in dry climates it extends to 1212 m (4000 ft.) (Henderson *et al.* 1989) (Figure 1). Soils are moderately moist and deep. Forest productivity is comparatively high and understory plant species thrive in this climate. Big game species use this zone for summer range at the upper elevations and for winter range elsewhere.

Floral Greens Production Potential

Many floral greens species are found in this zone. Dwarf Oregon-grape, salal and sword fern are all present. Evergreen huckleberry is plentiful, but beargrass and deer fern are not abundant.

Dwarf Oregon-grape is well-represented in most western hemlock associations. It is best represented in the vine maple (*Acer circinatum*) / vanillaleaf (*Achlys triphylla*) and the Pacific dogwood (*Cornus nuttallii*) / vine maple associations of this zone (Table 3). It is well-represented where it is dominant to co-dominant in the understory of this zone (e.g. western hemlock zone/: dwarf Oregon-grape/sword fern; dwarf Oregon-grape - Oregon oxalis; dwarf Oregon-grape; and salal - dwarf Oregon-grape associations). Constancy and coverage values remain sufficiently high for commercial harvest opportunities throughout most of this zone, except on the coolest/wet and warmest/dry sites.

Deer fern is less abundant in this zone compared to the Pacific silver fir zone, due to decreased precipitation and brief summer droughts. Deer fern is an indicator of moist to wet environments and is found in the cool-wet to warm-moist associations (e.g. western hemlock zone/: sword fern - Oregon oxalis; Alaska huckleberry - devils club; and Alaska huckleberry / Oregon oxalis associations). On microsites where miosture is excessive and sunlight is highly filtered, deer fern is of harvestable quality, but cannot always be harvested at commercial levels or for extended periods of time. The western hemlock zone is the warm-dry extreme of deer fern occurrence.

Salal is very common in the mesic to dry western hemlock associations. It grows on only a few of the cool-wet sites. Overall, the best salal for use as floral greens is harvested from plant communities

found in this zone. Moderate soil productivity, available soil nutrients, filtered sunlight and lengthened growing season allows salal to develop under near optimal growing conditions. Salal grows at near optimal levels where elevation averages 617 m (2025 ft.) (Henderson and Peter 1985), and precipitation levels are moderately low (Topik *et al.* 1986). On these sites, salal has 100 percent constancy with coverage between 34 and 64 percent. Where salal grows exceptionally well (e.g., western hemlock zone/: salal - dwarf Oregon-grape; salal - oceanspray (*Holodiscus discolor*); salal / Oregon oxalis; salal - evergreen huckleberry; salal / beargrass; and vine maple - salal associations) constancy approaches 100 percent with coverage values of 20 to 60 percent.

Sword fern quality and quantity increase in the western hemlock zone and surpass sword fern production in most other zones. On the Mount Baker Ranger District, the sword fern association is the most common association, representing 40 percent of the western hemlock zone (Henderson and Peter 1985). On cold-wet sites sword fern is often prevalent, attaining 100 percent constancy on many associations (e.g., western hemlock zone/: sword fern; sword fern - coolwort foamflower (*Tiarella trifoliata*); dwarf Oregon-grape - sword fern; and sword fern - salal associations) (Table 3). On drier western hemlock sites, where Pacific rhododendron and salal are dominant or co-dominant understory species, sword fern attains a constancy of over 60 percent, with moderate to low coverage values (e.g., western hemlock zone/: vine maple / salal; Pacific rhododendron - sword fern; Pacific rhododendron - dwarf Oregon-grape; Pacific rhododendron / salal; and Pacific rhododendron associations). In these associations, fronds can grow more than 150 cm (59 in.) in length with a deep green color (Haeussler and Coates 1986).

Evergreen huckleberry occurs in cool-moist to cool-dry environments in this zone. In three associations (western hemlock zone/: Pacific rhododendron; salal - evergreen huckleberry; and evergreen huckleberry associations), evergreen huckleberry has 100 percent constancy (Table 3). Evergreen huckleberry prefers the dry sites in the western hemlock zone.

Beargrass is not well adapted to the western hemlock zone. In the wettest climates, beargrass is rarely abundant enough for harvesting at commercial levels. Only on the extreme cool-dry sites of the western hemlock zone does beargrass attain adequate abundance for harvest. It attains harvestable levels generally where it is dominant to co-dominant in the understory layer (e.g., western hemlock zone/: Alaska huckleberry / beargrass; salal / beargrass; Pacific rhododendron / beargrass; and beargrass associations).

Management Considerations

The western hemlock zone includes some of the most productive forest land in the region (Topik *et al.* 1986, Halverson *et al.* 1986). Specific associations such as those possessing sword fern, devils club and Alaska huckleberry as indicators of the association, are more productive than others, but non-harvestable brush species cause competition problems (Henderson and Peter 1985). As discussed, this zone accommodates a wide variety of harvestable floral greens. The seral stage and the successional status dictates the floral greens harvest level. The best floral greens products, from a commercial perspective, are found in maturing forests with semi-closed canopies.

In some western hemlock associations, salal is represented in all stages of forest development, while evergreen huckleberry is present only in early to mid stages of forest succession. Commercially harvestable levels of both salal and evergreen huckleberry occur only during mid-successional stages of forest development. By maintaining forest conditions at or near the mid-successional stage of development, both products will remain harvestable.

Both sword fern and dwarf Oregon-grape occur in selected associations at all forest stand ages. But, the highest quality products are found growing in forests of mid to late successional status. When sword fern is subjected to increased amounts of direct sunlight by overstory removal, fronds decrease in quality and become dwarfed (Haeussler and Coates 1986). Like the salal and evergreen huckleberry example, maintenance of the forest site in the preferred successional status increases product quality and harvest quantity. Harvest treatments which retain a slightly higher canopy coverage than normally practiced allows for dual product management.

Certain forest associations within the western hemlock zone allow for forest management practices which provide acceptable conditions for salal, evergreen huckleberry, sword fern and dwarf

Oregon-grape. Use of the harvest technique described previously allows multiple product management, if regeneration sources remain viable. For example, consider the western hemlock/ salal - dwarf Oregon-grape association. This specific association is recognized on the Olympic National forest (Henderson *et al.* 1989), the Mt. Hood National Forest (Halverson *et al.* 1986), the Willamette National Forest (Hemstrom *et al.* 1987), and the Siuslaw National Forest (Hemstrom and Logan 1986), while similar associations are identified on the Gifford Pinchot National Forest (Topik *et al.* 1986), the Mount Baker-Snoqualmie National Forest (Henderson and Peter 1985), in the southern Oregon coast range (Bailey 1966, Bailey and Hines 1971), and in the central portion of the western Cascades in Oregon (Dyrness *et al.* 1976). This association is characterized by mesic habitats with moderate timber productivity. There are two general successional pathways, one dominated by Douglas-fir and the other dominated by western hemlock (Henderson *et al.* 1989). The successional tendencies of this association include both salal and dwarf Oregon-grape at all stages of development. Evergreen huckleberry is abundant in early to mid development while mid to late herb layer development is dominated by large populations of sword fern (Hemstrom and Logan 1986). Forest management considerations often include enhancement of soil nutrients, organic matter and controlling brush competition (Henderson *et al.* 1989).

Floral greens occur in various amounts in the western hemlock / salal - dwarf Oregon-grape association (Table 3). Dwarf Oregon-grape coverage values span 10 to 29 percent, with 100 percent constancy. Salal also attains 100 percent constancy, but has higher coverage values ranging from 31 to 63 percent. Sword fern is usually well represented with constancy ranging between 62 and 100 percent and coverage up to 24 percent. Evergreen huckleberry is usually less represented, with constancy values averaging 17 percent and coverage averaging 23 percent (Table 3).

As tree crown shading increases, dwarf Oregon-grape and evergreen huckleberry should become harvestable. However, if the canopy layer becomes too dense, it will tend to limit understory plant species. A moderate precommercial thinning will allow understory growth to increase coverage levels for a period of years. Following thinning, salal populations tend to increase in size and product quality improves.

As the forest stand matures, evergreen huckleberry occurrence decreases and sword fern populations increase. At forest stand maturity, salal, dwarf Oregon-grape, sword fern and small amounts of evergreen huckleberry are harvestable. Before evergreen huckleberry becomes scarce, a commercial thinning to simulate earlier seral conditions can maintain or increase evergreen huckleberry populations for several years.

Douglas-fir Zone

The Douglas-fir zone usually occupies south-facing slopes at mid to low elevations in the northern range and all except north facing slopes in the southern range of the western Cascades (Henderson *et al.* 1989). The environment is characterized as warm-dry with precipitation generally less than 1000 mm (40 in.) with frequent summer droughts (Figure 1). Snow accumulations tend to be minimal. Forest productivity is low compared to other forest zones of the region.

Special Forest Products Potential

Only dwarf Oregon-grape and salal appear harvestable in this zone. The salal association (Douglas-fir / salal) on the Olympic National Forest contains salal at 100 percent constancy and 56 percent coverage (Henderson *et al.* 1989). Dwarf Oregon-grape averages 85 percent constancy with only 15 percent coverage. A similar but drier association recognized in the central portion of the western Cascades in Oregon describes a salal - oceanspray association which includes dwarf Oregon-grape at 100 percent constancy and 19 percent coverage (Dyrness *et al.* 1976). Salal also has 100 percent constancy with 35 percent coverage (Table 3). The Willamette National Forest characterizes an oceanspray - dwarf Oregon-grape association on which dwarf Oregon-grape has 100 percent constancy and 26 percent coverage (Hemstrom *et al.* 1987). Both salal and sword fern are present with low constancy levels (Table 3). The Olympic National Forest has a drier oceanspray - baldhip rose (*Rosa gymnocarpa*) association (Henderson *et al.* 1989), which is similar in many respects to the oceanspray association identified in the western Cascades in Oregon (Dyrness *et al.* 1976). Dwarf Oregon-grape ranges in constancy from 88 to 100 percent, with corresponding coverage values of 4 and 16 percent. Salal constancy ranges from 23 to 62 percent, but coverage is very low, averaging below 5 percent (Table 3). In each Douglas-fir association,

sword fern and beargrass are represented with moderate constancy and low coverage values.

Management Considerations

Floral greens management on the Douglas-fir zone is primarily limited to considerations for salal and dwarf Oregon-grape. Because many of these sites are slightly mesic to dry, often on steep southern slopes, problems arise because of soil stability and erosion. Often soil erosion and soil instability concerns preclude commercial thinnings as a management option (Henderson *et al.* 1989). Floral greens management is primarily limited to mature and overmature stands which possess the desired product(s) at acceptable levels. Management activities are limited to product identification, inventory and monitoring of harvest.

Discussion

The western hemlock zone is not only the most accessible and most productive, but also possesses the highest potential for floral greens production. Salal, evergreen huckleberry, sword fern and dwarf Oregon-grape all flourish at near optimal growing conditions. This zone is also utilized extensively for timber production, which can easily be matched with floral greens production. The Pacific silver fir zone is not as productive overall as the western hemlock zone, but it is better suited to production of beargrass and deer fern. The mountain hemlock zone has the most productive beargrass sites, but accessibility is a limiting factor to intense management.

Certain steps are necessary to ensure proper management of floral greens. First, an identification of the forest site as it pertains to forest zones and specific plant associations is necessary. This identification allows characterization of typical management concerns, while helping to identify the floral greens products available on the site.

Second, forest land managers should consider the use of longer-term rather than shorter-term leases. Nearly half of the harvest leases in 1989 lasted only one year or less. The short-term nature of these leases was partially explained by the policies of the public agencies in the region (Schlosser *et al.* 1991). Conversely, many harvesters and producers are willing to enter long-term agreements with land owners/managers. Such long-term agreements are more desirable than short-term contracts because the incentive to overharvest in a given year is reduced.

Third, the lease should be advertised and offered to as many producers and harvesters as possible. The region has about 60 producers and over 5,400 harvesters. The Washington State Department of Natural Resources has offered at least some special forest product leases which are as long as 10 years in duration and are publicly auctioned (Schlosser *et al.* 1991). This process attracts many producers and harvesters and potentially higher lease revenues.

Finally, monitoring of floral greens populations should be conducted periodically to assess the effects of the harvest process. Little is currently known about the environmental impact of removing various amounts of understory biomass yearly or every other year.

Floral greens management is a relatively new consideration to land managers in the Pacific Northwest. By entering into floral greens harvest leases, net revenues can increase significantly. Opportunities exist for improved production and utilization of the resource.

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Book Review

A Field Guide to Mammal Tracking in North America. James Halfpenny, illustrations by Elizabeth Biesiot (Johnson Publishing Company, Boulder, Colorado, $13.95)

A Field Guide to Mammal Tracking in North America addresses a little-known subject. In our modern, technological society we have little use for a skill our forefathers may have relied upon for subsistence. Tracking wildlife is now limited to a minority of hunters, researchers, and naturalists. But with environmental awareness increasing in recent years, so has interest in wildlife study. As a result, many field guides have been published—mostly in the realm of ornithology. Less effort has been put foward concerning mammals, especially on tracks and signs. James Halfpenny attempts to provide a book on the subject in field-guide form, with a systematic approach to identifying tracks and interpreting trails.

The book is organized in four main parts. The author first provides an introduction which contains background information on the formation of tracks and trails. This includes basic anatomy of the mammalian foot, limb structure, and mechanics of locomotion. Particularly useful is a section describing the different types of gaits and resulting track patterns. The author also devotes a section to techniques in which he explains methods of collecting and preserving tracks, taking measurements, keeping a field journal, and step-by-step procedures for identifying tracks and interpreting trails. All important words are clearly defined, avoiding confusion of meanings which may result from commonly-used terms.

The second and largest portion of the guide consists of ten chapters, each of which is devoted to a particular taxonomic group of mammals. Each chapter describes track characteristics specific to that group, and along with life history information, aids the reader in distinguishing a track or trail to family, genus or species level. A chart is provided in the front of the book which shows key attributes of each group of mammals. With it one may find the group to which a particular track specimen belongs and quickly turn to the appropriate section by flexing the pages and locating the corresponding band on the margin. Likewise, another reference—a "track formula"—is provided at the bottom of each page which defines the basic traits of that group, such as number of toes on front and hind feet, relative size differences of front versus hind feet, and the likelihood of claws showing in the print. All portions in this section and throughout most of the book are well-illustrated and documented, showing common and uncommon examples of prints and patterns.

The third part of the book is designed as a teaching section. Illustrations of various mammal trails are provided, along with clues to engage the reader in learning to identify tracks and decipher the trail(s). Answers follow, with explanations as to the conclusion reached by the author.

A chapter regarding scatology concludes the guide, with texts and photographs describing characteristics of each group of mammals.

A Field Guide to Mammal Tracking in North America contains much useful information. At first glance, the format seems somewhat confusing for a field guide, but this is due in part to the rather extensive background of information provided. As with any instructional book, the reader must become familiar with the subject and the author's style, and this is no exception. A good background is imperative for understanding the basics of animal tracking. Once acquainted, the reader should have little difficulty in using the guide. Illustrations are helpful and well-done, but for one exception. Drawings in the self-teaching section tend to be somewhat vague and difficult to decipher.

An excellent feature of the book is found in the comparisons of characteristics between taxonomic groups, including those at the species level. This enables the reader to become cognizant of differences and similarities and aids in learning individual tracks and patterns.

Because the book is organized in more of an essay form, a reader may find it lacking somewhat as a field guide. However, it will serve as a useful reference for anyone interested in learning to identify and decipher mammal tracks and trails.

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Sixty-fifth Annual Meeting
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March 24-28, 1992,
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Effects of Stocktype, Shading, and Species on Reforestation of a Droughty Site in Southwest Oregon

Abstract

On hot, dry sites, shading may differentially increase survival of planted Douglas-fir according to seedling size, and Douglas-fir may differ from ponderosa pine in early survival and growth. We compared the survival and growth on a droughty, south-facing clearcut of Douglas-fir seedlings (1-0 container-grown plug and larger diameter 2-0 bareroot Douglas-fir seedlings, unshaded or shaded with cardboard shadecards at planting) and unshaded 2-0 bareroot ponderosa pine. Shading did not significantly increase survival of plugs, possibly because of a wetter than normal first summer, nor did shading affect growth of either stocktype 5 years after planting. According to linear contrasts, Douglas-fir bareroots remained significantly larger than plugs, but relative growth rates for the initially smaller plugs were significantly greater for diameter and volume. Survival and growth of pine tended to be better than that of Douglas-fir. Both species have potential for reforestation of similar harsh sites.

Introduction

Heat and drought have been perceived as barriers to reforestation with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in southwest Oregon (Franklin and Dyrness 1973). Heat kills planted conifer seedlings because of high soil surface temperatures that damage stem tissue near the soil surface (Moulopoulos 1947). South-facing sites are regarded as most likely to develop lethal soil temperatures. Although shelterwood overstories can reduce heat loads to below lethal levels on these sites (Childs and Flint 1987), clearcutting is sometimes preferred for reforestation because of pest management, cost, or other considerations. On clearcuts, silviculturists have shaded planted seedlings with cardboard shadecards to increase survival (Lewis *et al.* 1978). However, the need for shadecards may vary with seedling size, as well as with the seedling's environment. For example, in Greece, with a similarly dry growing season, larger conifer seedlings were damaged less by heat than were small seedlings (Moulopoulos 1947).

In southwest Oregon, two stocktypes of Douglas-fir are commonly planted: 1-0 seedlings (plugs) grown in containers for 1 year in a greenhouse, and larger 2-0 bareroot seedlings grown for 2 years in an outdoor nursery bed. The literature reports that shade from shadecards has increased survival of each stocktype individually (Hobbs 1982, Helgerson 1990), but 1-0 plugs and 2-0 bareroots have not been compared side by side to see whether they respond differently to shading under otherwise similar conditions. Our first objective was to determine whether shadecards affected survival and growth of these two stocktypes differently. This information could help foresters to more efficiently prescribe planting and shading of these two stocktypes.

Douglas-fir and ponderosa pine (*Pinus ponderosa* Laws.) typically occur together on low- to mid-elevation sites in southwest Oregon. Because of its greater resistance to drought (Franklin and Dyrness 1973), ponderosa pine is often regarded as better suited than Douglas-fir for reforestation of such sites. Our second objective was to determine whether the two species differed in their early survival and growth on a droughty south-facing slope. Little information exists comparing early survival and growth of these conifer species when planted on droughty sites.

Methods

The Salt Creek study site is located on holdings of the Medford District, Bureau of Land Management. It is within a south- to southwest-facing, 18-ha clearcut at 975 m elevation in the foothills of the Cascade Mountains, about 26 km northeast of Medford, OR. Slopes in our test area range from

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20 to 30 percent. The area receives approximately 760 mm of precipitation annually (Froehlich *et al.* 1982), with only about 130 mm falling between May 1 and September 30 (McNabb *et al.* 1982). Soils belong to the Geppert Series, a loamy-skeletal, mixed mesic, Dystric Xerochrept forming in colluvium from andesite and breccia (personal communication, Nicola Giardina, USDA Soil Conservation Service, Medford, OR, unpublished report on file).

The site is located in the Mixed-Conifer Zone (Franklin and Dyrness 1973), belonging to the PSME/RHDI/CYGR Association of the Douglas-fir Series (Atzet and McCrimmon 1990). Douglas-fir site index (McArdle *et al.* 1961) was estimated at 60 feet on a 100-year base (personal communication, Terry Tuttle, Medford District, BLM, data on file). This site had been classified by the Medford District as difficult to reforest because of heat and drought; it is typical of other foothill areas.

The site was clearcut and burned for site preparation in 1982. In 1983, five seedling treatments were set out as a randomized complete block design with three replications (Sokal and Rohlf 1981). The five treatments consisted of Douglas-fir 1-0 plugs and 2-0 bareroot seedlings, either unshaded or shaded with shadecards at planting, and 2-0 bareroot ponderosa pine (unshaded). The plugs were grown in 164-cm^3 containers.

Seed for all seedlings came from within the surrounding seed zone; that for the Douglas-fir plugs came from 790 m elevation and that for all other seedlings from 760 m. The seedlings were planted on March 8, 1983, at approximate 2.4-m spacing within each 20- by 20-m treatment plot. Fifty seedlings were tagged in each treatment plot for subsequent recording of survival and growth; thus each of the five treatments was represented by 150 seedlings. Shadecards were installed within 1 week of planting. Weed presence was reduced shortly after planting by application of atrazine with a backpack sprayer to control herbs, and near the start of the 1985 and 1987 growing seasons by installations of paper mulches around seedlings and by cutting woody vegetation within test plots.

Survival, seedling heights (to distal end of uppermost live bud), and diameters (25 mm above soil) were measured on live seedlings immediately after planting and at the end of each of the first five growing seasons. We first ascertained treatment effects by analysis of variance, regarding time of measurement as a subplot of seedling treatment to determine whether treatment means changed according to measurement time (Cochran and Cox 1957). The planned comparisons between shading and stocktypes for Douglas-fir, and between the pine and all Douglas-fir, were tested with linear contrasts (Sokal and Rohlf 1981). Unplanned differences among the five seedling treatments were identified with the Scheffé test (Sokal and Rohlf 1981). Dependent variables were: survival; height (H); diameter (D); stem volume (V, calculated according to the formula for a cone, $V = \pi D^2 H/12$); and relative growth rates (RGR) for D, H, and V. Here, $RGR = \ln size_5 - \ln size_{planted}$, where $size_5$ is size at the end of the fifth growing season and $size_{planted}$ is size at planting (Harper 1977). Survival means were arc-sine transformed (Sokal and Rohlf 1981), which increased the normality of the residuals. All analyses were conducted on SAS (SAS Institute 1987) and screened for statistical significance at $p < .05$.

Results and Discussion

Survival

A significant interaction between treatment and time ($p < 0.05$) showed that seedling treatment affected survival over time. After five growing seasons, the linear contrast between Douglas-fir stocktypes showed that the 2-0 bareroots survived significantly better than the 1-0 plugs, but shading with shadecards did not significantly increase survival; shading had an effect only at the $p = 0.16$ level (Table 1). The linear contrasts between species showed that ponderosa pine survived significantly better than all Douglas-fir seedlings taken together.

This lack of shading effect was unexpected because, in previous separate studies, shading had increased survival of both Douglas-fir stocktypes (Hobbs 1982, Helgerson 1990). We expected the plugs, in particular, to benefit from shading because of their significantly smaller mean diameters at planting (3.6 mm for plugs vs. 5.8 mm for bareroots). The plugs did show a larger survival difference after five growing seasons—75 percent for shaded vs. 57 percent for unshaded plugs, compared with 86 vs. 84 percent for bareroots—but the interaction between shading and stocktype was not significant (Table 1).

The Sheffé comparison, a more conservative test than linear comparisons, showed two overlapping groups of 5-year survival means at the $p = .05$

TABLE 1. Significance levels (probability of a greater F-ratio) for linear contrasts by mean survival, stem height, diameter, volume, and relative growth rate (RGR) 5 years after planting. RGR = $\ln size_5 - \ln size_{planted}$.

	Linear contrast			
	Douglas-fir			
Variable	Shade	Stocktype	Shade x stocktype	Douglas-fir vs. pine
Survival	.16	.01	.24	.02
Height	.41	.002	.91	.01
Diameter	.78	.004	.36	.0001
Volume	.74	.04	.87	.0001
RGR height	.55	.009	.95	.0007
RGR diameter	.06	.0001	.74	.0002
RGR volume	.09	.0009	.83	.0004

level: all seedling treatments other than the unshaded plugs; and all Douglas-fir, excluding the pine (Figure 1a). This division shows that the only significant difference in survival among the five seedling treatments was between the 2-0 bareroot ponderosa pine and the unshaded 1-0 Douglas-fir plugs.

On south-facing slopes, heat damage to planted seedlings usually occurs during July or August, when soil surface temperatures reach maxima (Childs and Flint 1987). However, the absence of anticipated heat damage may be attributable to wetter than normal growing conditions (Gordon 1970). Medford precipitation totals for the months of July and August, 1983, were respectively in the 86th and 97th percentiles, according to records from 1913 to 1988 (personal communication, Mike Brooks, Medford Office, U.S. Weather Service, NOAA; data on file). Thus, the effects of shading on survival of Douglas-fir might have been more pronounced had the 1983 summer been more typically dry (Flint and Childs 1987).

The post-planting application of atrazine could have reduced survival of the plugs by its entry into their porous rooting medium, and shadecards could have reduced the exposure of adjacent seedlings. Although the mortality expected from atrazine can be small (Bruce Kelpsas, Northwest Chemical Corporation, Salem, OR, unpublished data), it is possible that increased exposure to atrazine contributed to the lower survival of the unshaded plugs.

Growth

Significant time by treatment interaction terms showed that seedling heights, diameters, and stem volumes varied significantly over time according to seedling stocktype and species. Linear contrasts showed no significant differences between unshaded and shaded Douglas-fir in mean height, diameter, volume, or growth (RGR) 5 years after planting (Table 1). This similarity suggests that shadecards did not affect 5-year growth of the Douglas-fir seedlings, a result that is consistent with other work (Helgerson 1990).

When planted, the bareroot Douglas-fir were significantly larger in diameter and volume (5.6 mm, 2.6 cm^3) than the plugs (3.6 mm, 1.0 cm^3), but were within 1 mm of the same height. After five growing seasons, significant linear contrasts (Table 1) showed that bareroots were significantly larger in height, diameter, and volume. According to significant contrasts of RGRs (Table 2), the bareroots outgrew the plugs in height, but the plugs outgrew the bareroots in diameter and volume.

When planted, the ponderosa pine were significantly shorter than the average of all Douglas-fir stocktypes, but pines had approximately the same diameter and volume as the 2-0 bareroot Douglas-fir. After five growing seasons, the linear contrasts (Table 1) of mean sizes (Figure 1) and RGRs (Table 2) showed that the pines were significantly larger and had grown more rapidly than Douglas-fir in height, diameter, and volume.

The more conservative Scheffé comparison did not show differences in sizes or RGRs associated with Douglas-fir stocktypes or shading after five growing seasons. However, it showed pine to be significantly larger than all Douglas-fir in diameter and volume and significantly taller than unshaded plugs (Figure 1b, 1c, 1d). The pine significantly surpassed the 1-0 plug Douglas-fir in height growth, and surpassed all 2-0 bareroot Douglas-fir in diameter and volume growth.

In 1986, the mean sizes of the 2-0 bareroot Douglas-fir and pine in our plots were very close to those for similar 2-0 bareroots on another portion of the site, where cattle grazing was intensive (Doescher *et al.* 1989). This similarity indicates that weed control by controlled cattle grazing and the repeated mulching and clipping of herbs and brush in our study may similarly affect early seedling growth.

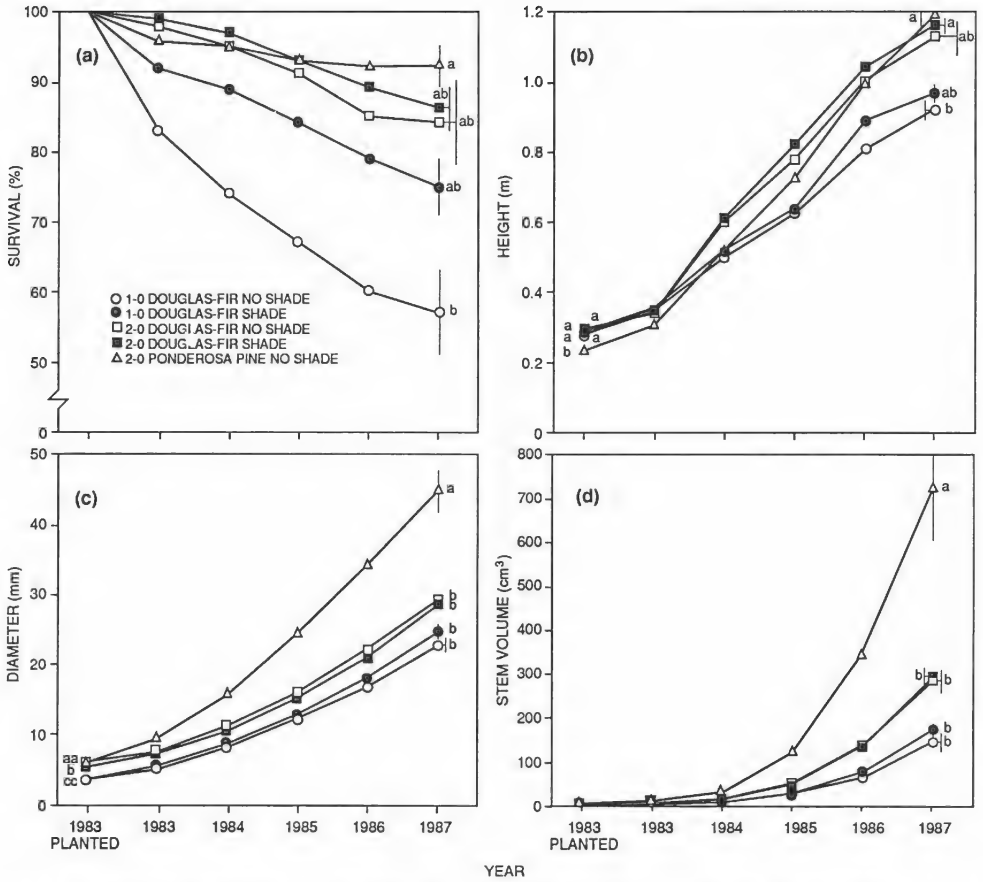

Figure 1. (a) Mean survival (percent), (b) stem height (m), (c) diameter (mm), and (d) volume (cm^3) at planting and at the end of the first five growing seasons. Letters denote differences among means at the p = .05 level according to the Scheffé comparison; vertical bars denote standard error (n = 3).

TABLE 2. Mean relative growth rate (RGR) for stem height, diameter, and volume according to seedling type. Letters denote differences between means in each row at p = 0.05 according to the Scheffé test.

	Douglas-fir				Ponderosa pine
	1-0 plugs		2-0 bareroots		2-0 bareroots
	unshaded	shaded	unshaded	shaded	unshaded
Height	1.173a	1.203a	1.357ab	1.394ab	1.613b
Diameter	1.813ab	1.904a	1.560c	1.625bc	1.983a
Volume	4.940ab	5.139ab	4.505b	4.757b	5.596a

Conclusions

Both Douglas-fir and ponderosa pine appear to be suited for reforestation after clearcutting on the droughty sites typified by this study. The consistently better survival and growth of the pine five growing seasons after planting indicates that pine may become established more quickly than Douglas-fir.

For Douglas-fir, stocktype affected survival and growth more than did shading; the lower-cost 2-0 bareroots survived and grew better than the 1-0 plugs. When available, the bareroots appear to offer more cost-effective reforestation.

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Achene Dispersal in Yellow Starthistle (*Centaurea solstitialis* L.)

Abstract

Rangeland infestations of yellow starthistle (*Centaurea solstitialis* L.), a facultative winter annual from the Mediterranean region, increased more than 60-fold in southeastern Washington between 1954 and 1964. Studies were begun in the early 1960s to better understand the ecology of yellow starthistle as an invading species. This paper reports the results of one of those studies that investigated the role of wind in dispersal of plumed achenes by trapping achenes downwind from a planting of yellow starthistle. Achenes were collected in traps spaced 0.3, 0.6, 1.2, 2.4, 4.9 and 9.8 meters from the perimeter of the seed source for 11 days in September. Temperature, relative humidity, dew point, total wind, wind gusts, precipitation and evaporation were recorded. Ninety-two percent of the achenes fell within 0.6 m and 48% fell within 0.3 m of the source. A combination of gusty wind and dry conditions maximized achene dispersal. Total achene dispersal was highly correlated with the daily maximum saturation deficit multiplied by the maximum wind gust per day ($r = 0.87$). Predation by seed-eating birds reduced achene numbers and may have increased dispersal distances. The significance of this research is that although wind normally does not move achenes long distances, it serves to fill intervening space between occasional plants and increase populations by persistently advancing the perimeter.

Introduction

Yellow starthistle (*Centaurea solstitialis* L.), a noxious weed that has invaded rangelands in the western United States, is unpalatable to livestock in all but its rosette and bolting stages and has sharp spines on its flower heads that deter grazing animals and recreationists. It is toxic to horses (Kingsbury 1964). Yellow starthistle was introduced in the Whiskey Creek drainage of Columbia and Walla Walla counties in southeastern Washington in the early 1900s as a contaminant in alfalfa seed (Roché 1965). In Columbia County, the yellow starthistle population which was estimated at 60 ha in 1954 had spread to 4,000 ha by 1964 (Roché 1965). By 1987, yellow starthistle was reported on nearly 18,000 ha in Columbia County and approximately 25,000 ha in adjacent Walla Walla County (Roché and Roché 1988). Field observations found that yellow starthistle seedlings grew principally in and near the debris of the previous year's yellow starthistle plants. Apparently most achenes fell close to the parent plant which should result in a relatively slow rate of spread, contrary to the rapid expansion observed after 1954. This investigation of the natural course of yellow starthistle dispersal, particularly the movement of achenes by wind, was one part of related studies on the ecology of yellow starthistle (Roché 1965).

Methods and Materials

The study was designed to monitor weather conditions and distance of achene dispersal by wind under normal conditions at achene maturity. Yellow starthistle was established 1.2 m apart in a grid pattern in two blocks of 100 plants each (12 m by 12 m square blocks) in a clean cultivated nursery planting in Pullman, Washington. A series of 6 traps were placed in a line perpendicular to the leeward side of the yellow starthistle planting. The traps were 0.3, 0.6, 1.2, 2.4, 4.9 and 9.8 meters from the edge of the block of yellow starthistle. This series of traps was replicated 10 times with replicates 3.6 m apart. Seed traps were constructed from coffee cans by replacing can bottoms with a 30 mesh Saran™ plastic screen funnel attached by 3M™ cement. The can was inverted, using the lid for a bottom that could be conveniently removed for achene counts. The opening of each can was 12.75 cm in diameter for an area of 127.7 cm^2.

The yellow starthistle plants were allowed to flower and by September were releasing mature achenes. On 11 September 1963 the traps were set in the ground so that the top of the trap was flush with the soil surface in the positions described above. The soil in the trapping area was kept free of vegetation. Accumulated achenes were removed from the traps and counted on 12, 13, 14, 16, 18, 21, 22, and 23 September. By that date peak dispersal of achenes had been reached, based on observation of empty seed heads in the planting. The number of achenes and hours per trapping period were adjusted and reported as total achenes per 24 hours.

Weather conditions were recorded during the trapping period, including temperature, relative

humidity, dew point, total wind, wind gusts, precipitation and evaporation. Total wind was recorded by a totalizing anemometer in the trapping area. Other weather data were obtained from the Moscow-Pullman Airport, approximately 1.5 km distant but within the same drainage, and the U.S. Department of Agriculture Plant Materials Center, about 300 m across the drainage floor from the study area. Saturation deficit was calculated.[1]

To assess the fate of the known number of achenes that fell 0.3 m from the edge of the starthistle planting, I counted the yellow starthistle seedlings and extracted the achenes from the debris and the top 2.5 cm of soil the following spring on 6 May.

Results and Discussion

Yellow starthistle produces two types of achenes. The florets in the outermost ring in each head produce plumeless achenes which are retained in the head until the phyllaries fall off after repeated wetting and drying during the fall and winter. Achenes produced by all the other florets are plumed by a double row of divergent, fine white pappus bristles, 3 to 4 mm long, plus a central short brushlike crown. As the achenes mature, the receptacle dries and contracts. The phyllary bracts also dry and contract, forcing the detached achenes up to a free position atop the head. Exposed to the air, the pappus dries and separates the achenes. Movement of the plant, usually by gusts of wind, dislodges and disperses the achenes. Moisture recloses the phyllary bracts, retaining the achenes. This mechanism is common among Asteraceae, particularly in Cynareae (Smith and Kok 1984, Sheldon and Burrows 1973). All of the yellow starthistle achenes dispersed in the trapping period were plumed.

The number of achenes per trap decreased rapidly with increasing distance from the source (Table 1); 92% of the trapped achenes were within 0.6 m of the perimeter of the stand. Traps placed at 0.3 m netted 48% of the total. No achenes were trapped 9.8 m from the source. This pattern was consistent with models for wind dispersal of winged or plumed seeds (Burrows 1973, Greene and Johnson 1989, Sheldon and Burrows 1973 and Smith and Kok 1984). Yellow starthistle has a small pappus relative to the size and weight of its achene and is generally released from a position less than 1 m in height.

A comparison of achene dispersal (Table 1) and weather data (Table 2) showed that saturation deficit was more important than relative humidity or wind. There was not a significant correlation of minimum relative humidity with achene dispersal to 0.3 m ($r = 0.68$). Maximum saturation deficit correlated with achene dispersal per day to 0.3 m ($r = 0.82$, $P \leq .05$). Achene dispersal was not correlated with wind alone, neither with total wind in km per day ($r = -0.19$) nor with maximum wind gusts in km per hour ($r = 0.19$). However, a combination of gusty wind and dry conditions maximized achene dispersal. Total achene dispersal was highly correlated with the daily maximum

[1]Saturation deficit = vapor pressure (in mm) − (vapor pressure X relative humidity (decimal)).

TABLE 1. Mean numbers of achenes of yellow starthistle (*Centaurea solstitialis*) collected in traps by distance and trapping period. Since trapping periods were not uniform, achenes per date are also adjusted to a 24-hour period.

Date	Hours in trapping period	Distance from source (m)						Total achenes per date	Adjusted to 24 hours
		0.3	0.6	1.2	2.4	4.9	9.8		
9-12	21	48.9	56.1	3.3	0.2	0.0	0.0	108.5	124.0
9-13	25	110.2	117.6	35.7	4.5	1.8	0.0	269.8	259.0
9-14	24	5.3	3.9	0.8	0.2	0.1	0.0	10.3	10.0
9-16	35	3.1	1.7	0.3	0.0	0.0	0.0	5.1	3.6
9-18	49	5.3	8.2	0.4	0.1	0.0	0.0	14.0	7.0
9-21	60	76.0	77.7	1.6	0.0	0.0	0.0	155.3	62.2
9-22	26	60.1	39.4	0.9	0.0	0.0	0.0	100.4	92.6
9-23	26	63.3	40.6	8.0	1.1	0.2	0.0	113.2	104.4
TOTAL		372.2	345.2	51.0	6.1	2.1	0.0		

TABLE 2. Climatic conditions during achene collection period (12 to 23 September 1963) at Pullman, Washington: temperature (TEMP), relative humidity (R.H.), saturation deficit (S.D.), wind as total km and gusts, precipitation (PPT.), and evaporation (EVAP.).

Date	TEMP °C mean	TEMP °C high/low	R.H. % minimum	S.D. mm maximum	WIND km/day total	WIND km/hr gusts	PPT. mm	EVAP. mm
9-12	26.8	33/18	22	25.6	73	24		5.6
9-13	18.5	31/13	29	23.1	224	40	6.9	4.7
9-14	15.1	17/12	56	6.4	335	56	8.9	4.0
9-15							0.3	3.8
9-16	11.1	17/8	56	6.4	229	16	1.8	1.0
9-17							1.9	0.7
9-18	14.1	22/8	39	11.7	161	16		2.0
9-19								2.9
9-20								3.2
9-21	19.2	26/10	27	18.3	169	8		3.4
9-22	26.0	27/24	27	18.3	261	16		3.2
9-23	17.1	26/13	36	16.1	210	16	1.0	3.5

saturation deficit multiplied by the maximum wind gust per day ($r = 0.87$, $P \leq .01$).

During 11 days of seed dispersal the mean of total achenes collected 0.3 m from the source was 372.2 per trap (127.7 cm^2) (Table 1). This number represented 291.5 achenes per dm^2. The following spring on 6 May, the mean density of the volunteer yellow starthistle population was 32.3 seedlings per dm^2. Analysis of the debris and top 2.5 cm of soil yielded only 0.2 achenes per dm^2. Numerous yellow starthistle seed hulls were observed, indicating that many of the remaining achenes had been consumed by birds. One yellow starthistle plant was found at a distance greater than 9.8 m from the parent material. That achene and others may have been moved by birds, rodents, insects or whirlwinds.

Seed Predation by Birds

During seed dispersal, birds fed heavily on yellow starthistle achenes, with an estimated 100 or more individuals feeding in the nursery daily. Species included ring-necked pheasants (*Phasianus colchicus* L.), California quail (*Callipepla californica* Shaw), house finches (*Carpodacus mexicanus* Müller), and American goldfinches (*Carduelis tristis* L.), of which house finches were the most abundant. Bird crops were analyzed by sampling 12 house finches. Each finch had hulled yellow starthistle achenes in its crop, with the number of achenes per crop ranging from 6 to 333. The number of achenes was probably indicative of the length of feeding time. The finch with 333 achenes in its crop was filled into its throat.

Birds have been implicated in both long and short distance dispersal of weed seeds (Aison *et al.* 1984, Blockstein *et al.* 1987, and Thill *et al.* 1986). The birds feeding on yellow starthistle achenes in the nursery fall into two groups with basic differences in digestive systems and feeding habits. Goldfinches and house finches hull or shell seeds and have weaker gizzard musculature than pheasants and quail who consume intact seeds (Ziswiler and Farner 1972). Pheasants and quail remain within a relatively small territory (Thill *et al.* 1986) while finches feed in flocks and range widely from one abundant food source to another (Newton 1972). Achenes taken by finches would probably remain viable only if they were accidently swallowed or dropped without being hulled. Some viable achenes may pass through the digestive tract of pheasants (Thill *et al.* 1986).

Most achenes consumed by birds are lost to the regeneration pool. However, since yellow starthistle seed production is far in excess of the number needed to maintain and expand the population, predation may simply remove achenes that were doomed to stress related mortality (Harper 1977).

Expansion of yellow starthistle populations by wind-dispersed achenes alone is a relatively slow

process. But large numbers of achenes moved short distances by wind can blanket an area following introduction of a few achenes widely dispersed by whirlwinds, birds, other animals or vehicles.

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Foothill Oak Woodlands of the Interior Valleys of Southwestern Oregon

Abstract

We describe the vegetation of the Oregon white oak woodlands found on foothills in the interior valleys of southwestern Oregon. Reconnaissance plots were used to sample the vegetation. Cluster and gradient analyses were used to identify community types, examine relationships between community types, and relate community composition to the environment. Five community types were recognized from a data set of 53 plots. Four of these community types were ordered along a precipitation gradient, while the fifth occurred on ridge lines and rock outcrops. Floristic composition and structure of these woodlands have been disturbed by fire suppression, livestock grazing, introduction of alien species, and firewood harvest. Without changes in land management, the oak woodlands characteristic of southern Oregon will diminish.

Introduction

Low elevations within southwestern Oregon are bounded by oak woodlands, which are transitional to savannas and grasslands. These woodlands are the lower elevation limit for forest vegetation in the region (Waring 1969, Franklin and Dyrness 1973). *Quercus garryana* (Oregon white oak), with a natural range from Vancouver Island to southern California (Griffin and Critchfield 1972), dominates the foothill and valley bottom woodlands. These oak woodlands reflect a climatic transition between mesic lowlands of the Willamette Valley and northwestern Oregon (where *Q. garryana* reaches optimal development), and xeric lowlands within the interior valleys of northern California. This unique environment supports the convergence of taxa common to both California and Pacific Northwest floristic provinces (Stebbins and Major 1965, Raven 1977).

Many bottomland stands were cleared for agriculture. Stands on less fertile upland sites have often been utilized for livestock grazing, and more recently for fuel wood. We assume overstory canopy structure and composition of these sampled stands are near pristine but little is known about original understory species composition. Disturbance from livestock grazing, fire suppression, and wood harvesting have initiated the establishment of non-native herbaceous species that competitively displace many of the native taxa.

The objectives of this study were to: 1) document the major plant community types that occupy these foothill woodlands, determining their composition and structure; and 2) interpret the environmental factors influencing their distribution.

Study Area

The interior region of southwestern Oregon is comprised of the Umpqua and Rogue River watersheds (Figure 1). The area is a complex mixture of valleys, foothills, and mountains. Major mountain ranges border the region on the east, south, and west. The northern edge of the Umpqua River watershed forms the northern boundary. Elevations typically range from 150 to more than 1300 m within the region.

The near-Mediterranean climate is characterized by winter rains and dry, hot summers (Figure 2). Precipitation maps published for the area (Froehlich *et al.* 1982, McNabb *et al.* 1982) show a complex pattern of rainshadow effects, but an overall trend of decreasing precipitation from north to south and from west to east. Roseburg (Figure 2) receives an annual mean of 800 mm of precipitation, while Medford receives on average only 400 mm. The dry season typically lasts five months (May-September). Occasional frosts can occur throughout much of the year, although mean minimum temperature drops below freezing only at the Medford station.

The region overlaps portions of both the Klamath Mountain Province and the Western

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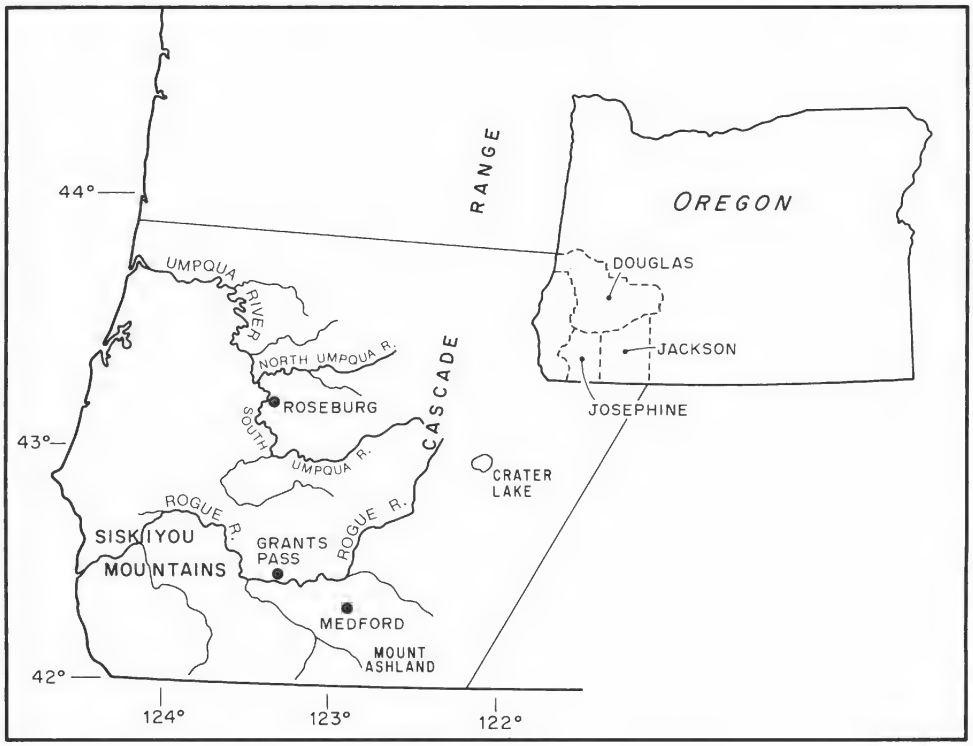

Figure 1. Generalized map of southwestern Oregon, detailing the study area.

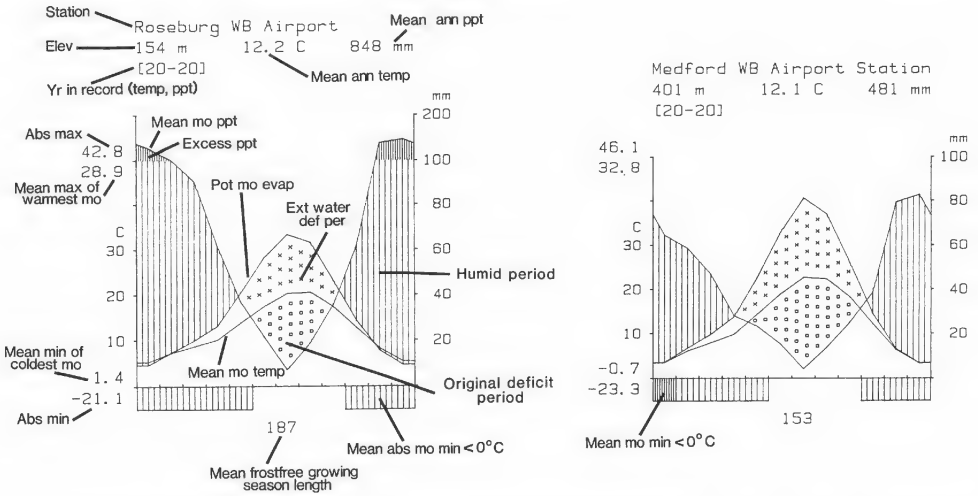

Figure 2. Climate diagrams for Roseburg and Medford, Oregon, patterned after Walter (1985). To better represent the dry season these diagrams were modified to include a potential evapotranspiration curve (Schreiber 1977). Precipitation and temperature data are averages from 1967 to 1987. Extremes are extracted from the whole weather record of more than 100 years for each station. Weather data supplied by K. Redmond, former State Climatologist, Oregon State University.

Cascades Province (Franklin and Dyrness 1973), and is geologically diverse. Important parent materials include tuffs and andesites in the Western Cascades Province and metamorphosed sediments and volcanics, ultramafics, and granitics in the Klamath Mountain Province (Wells and Peck 1961).

Soils are very diverse, with more than 50 series identified (Stearns-Smith and Hann 1986). Soils in the Western Cascade Province are classified as Xerumbrepts or Haplumbrepts, while those in the Klamath Mountain Province fall into a diverse range of suborders related to parent material (Franklin and Dyrness 1973).

Evergreen forests dominate the regional vegetation (Franklin and Dyrness 1973). At lower elevations both evergreen broadleaf species and conifers occur, while at upper montane and subalpine elevations conifers are the sole tree species. Important lower elevation taxa include conifers such as: *Pseudotsuga menziesii* (Douglas-fir), *Abies concolor* (white fir), *Pinus ponderosa* (ponderosa pine), and *Calocedrus decurrens* (incense-cedar) and broadleaf species such as: *Quercus garryana, Q. kelloggii* (California black oak), *Arbutus menziesii* (madrone), and *Lithocarpus densiflorus* (tanoak).

Quercus garryana is an important woodland and forest species at lower elevations along valley margins and in the foothills. It may be a codominant with *Q. kelloggii,* for example, or be the exclusive species in woodlands (defined as a community type with trees generally growing in open spacing with a well-developed understory). As a forest tree, it occurs in association with a variety of broadleaf and coniferous taxa.

Methods

Sampling Methods

The fragmented, highly disturbed oak woodland landscape in southwestern Oregon possesses special problems for the development of a vegetation classification. We began by identifying potential sample sites using aerial photographs. Each site was visited and sampled if judged to be suitable. Sample criteria included (1) no visible signs of current or recent livestock grazing; (2) no visible signs of recent fire; (3) presence of a mature overstory with trees at least 100 years old and canopy cover greater than 20 percent (i.e., a woodland or forest); and (4) dominance or codominance of *Q. garryana* in the overstory and seedling and sapling size classes.

Data at each plot were collected using an efficient reconnaissance-oriented method (Franklin *et al.* 1970) similar in many respects to the relevé (Braun-Blanquet 1963). Each plot was representative of the stand with no obvious vegetation discontinuities. A plot consisted of a 500 m^2 circle, within which a complete tally of all vascular plants was made. Projected, relative crown cover was ocularly estimated for each species. In addition, cover for each tree species was estimated in each of five size classes (<1.4 m tall; $0 <$ dbh < 1 dm; 1-3 dm dbh; 3-10 dm dbh; and >10 dm dbh). Tree and snag basal area was estimated by prism. General stand composition and structure was described by estimating cover in each of six lifeform strata [moss and lichen, herbaceous, low shrub (<0.5 m), tall shrub (>0.5 m), reproduction (trees <3 m), and trees greater than 3 m]; counting species in all strata except mosses and lichens; estimating relative cover of litter; and measuring the height of a stand dominant. Nomenclature follows Munz (1973) and Hitchcock and Cronquist (1973).

Physical parameters recorded: elevation, aspect, slope, topography (including slope position and horizontal and vertical configuration); and ground cover for loose rock, bedrock, and bare mineral soil surface. Annual and dry season (May-September) precipitation values were interpolated from isohyetal lines for each plot on precipitation maps produced by Froehlich *et al.* (1982) and McNabb *et al.* (1982). A 40 cm soil pit was excavated at each plot to examine the litter layer and upper soil horizons. Litter and soil depth were recorded along with proportions of gravel and stones in the upper 40 cm. Soil pH was assessed using indicator dyes.

Analytical Methods

The principal goal of this study was to identify plant community types by examining vegetation data for cluster pattern. A community type is an abstract unit of vegetation that is defined by physiognomic, floristic and dominance characteristics. All stands assigned to a community type share a similar physiognomy, flora, and relative dominance of component species. The flora, composed of native and non-native taxa, reflect current environmental conditions and may not persist over extended time.

The traditional phytosociological method of identifying community types in a data set is the ordered table (Westhoff and van der Maarel 1978). Several computer programs now exist that automate both the ordering of phytosociological tables and the identification of types within the ordered table. A computer program called TWINSPAN (Two Way INdicator SPecies ANalysis; Hill 1979a) was used initially to cluster the data and identify tentative community types. Indicator species analysis is a type of cluster analysis. TWINSPAN was used because of its speed, efficiency, and ability to handle large data sets. The initial types were subsequently refined using gradient analysis and manual table-sorting techniques. Eight initial types were interpreted from the TWINSPAN results. Examination of the floristic data in ordered tables (program ASSTAB, written by B. Smith), the environment data (elevation, aspect, annual, precipitation, etc.) and the display of data in ordination space resulted in the collapse of the eight initial types into five. These types were judged as being relatively distinct. This process of refining the initial types using manual techniques incorporates judgment of the ecological indicator value of the species involved. This kind of judgment cannot be incorporated into the automated tools that only use the species abundance data. As such, this process becomes more art than science.

Detrended correspondence analysis (DCA), as implemented in the computer program DECORANA (Hill 1979b), was used in community type designation to determine factors influencing community distribution. Ordinations of the individual plot data were used to help refine the classification. Each plot was coded according to the community type to which it was allocated, thereby allowing visual inspection of community type distribution in ordination space. Once community type membership was finalized, ordination of composite data (the average abundance of all species that occur in the individual plot data assigned to a specific community type) examined relationships between types in an attempt to understand the underlying factors controlling the distribution of types. Each type in the final classification was represented by one composite plot. Ordination scores from the composite ordinations were rank correlated, using Kendall's *tau* (Grieg-Smith 1983), with physical variables precipitation (annual and dry season) and elevation to identify potential underlying determinants of vegetation pattern.

Diversity, ubiquity, and similarity patterns were analyzed with AID-N (Overton *et al.* 1987). Richness and dominance were the two components of diversity examined. Richness and dominance were calculated for each plot and then averaged for each community type. Richness, N_1, was simply expressed as number of species (Hill 1973). N_2 was the dominance index used (Hill 1973), and is the reciprocal of Simpson's *lambda* (Hill 1973). Ubiquity refers to a set of measures that index the distribution of individual species across a data set. Two measures of ubiquity were used. The first (U_0) was constancy and the second (U_2) is calculated as:

$$U_{2(i)} = \frac{\left(\sum_{j}^{n} p_{ij}\right)^2}{\sum_{j}^{n} p_{ij}^2}$$

where n is sample size and P_{ij} is relativized datum for attribute $_i$ on sample-unit $_j$ (Overton *et al.* 1987). This equation is of the same form as N_2 except that the summation occurs across all occurrences of one species, while for N_2 the summation is across all species in one sample unit. U_2 is normally expressed, like constancy, as a percentage of sample size:

$$U_{2(i)} = U_{2(i)} \times \frac{100}{n}$$

where n is sample size.

Results

Fifty-three plots containing a total of 88 species were sampled. The species have the following life-form spectrum: 7 trees, 8 shrubs, and 73 herbs and grasses. The 5 most ubiquitous species (in descending order) are *Q. garryana*, *Cynosurus echinatus* (hedgehog dogtail), *Rhus diversiloba* (poison-oak), *Poa trivialis* (roughstalk bluegrass), and *Bromus carinatus* (California brome) (Table 1).

Elevations range from 160 to 1000 m, with an overall mean of 610 m. Predicted mean annual precipitation ranges from 500 to 1750 mm with a corresponding dry-season rainfall of 100 to 220 mm. Slope inclinations are generally below 30% and have southerly exposures.

Classification

Five community types are recognized using TWINSPAN (Table 1): *Quercus garryana/Bromus*

TABLE 1. Constancy[1] (Con) and characteristic cover[2] (Cov) for selected species[3] by community type. Species ordered alphabetically within growthform strata.

	Quercus garryana									
					Pseudotsuga menziesii					
	Bromus carinatus		*Cynosurus echinatus*		*Festuca ovina*		*Elymus glaucus*		*Cercocarpus montanus*	
Number of plots	17		13		10		10		3	
	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov
Tree Layer										
Arbutus menziesii	24	14	15	2	50	1	50	7	67	18
Cercocarpus montanus	24	1	–	–	30	T	10	1	100	17
Pinus ponderosa	35	10	31	3	60	5	10	T	67	10
Pseudotsuga menziesii	18	8	15	1	80	7	90	5	33	T
Quercus garryana	100	32	100	38	100	34	100	33	100	52
Quercus kelloggii	18	5	15	8	20	3	30	23	–	–
Tall Shrub Layer										
Ceanothus cuneatus	71	2	46	6	30	5	10	T	100	12
Rhus diversiloba	82	8	85	4	100	4	90	12	–	–
Symphoricarpos albus	24	2	38	T	60	T	20	T	33	T
Low Shrub Layer										
Lonicera hispidula	35	T	8	T	50	1	20	T	33	T
Herb Layer										
Anthriscus scandicina	94	2	85	9	60	3	80	4	33	T
Bromus carinatus	100	12	15	1	30	2	10	T	–	–
Bromus mollis	29	3	54	6	30	10	20	6	–	–
Cynosurus echinatus	82	6	85	20	80	4	90	8	67	T
Dactylis glomerata	–	–	15	8	–	–	70	13	–	–
Daucus pusillus	–	–	–	–	–	–	–	–	67	6
Elymus glaucus	18	1	62	T	60	2	90	7	67	T
Festuca myuros	–	–	8	20	–	–	–	–	–	–
Festuca pratensis	12	T	38	8	10	T	10	5	–	–
Festuca occidentalis	6	1	–	–	20	20	50	12	33	T
Festuca ovina	53	9	8	5	70	10	–	–	–	–
Marah oreganus	6	T	8	T	10	T	–	–	67	12
Poa trivialis	65	7	54	7	60	6	30	7	33	T
Pteridium aquilinum	–	–	–	–	–	–	10	T	33	35
Sanicula graveolins	82	T	23	T	60	T	90	T	–	–

[1]Occurrences expressed as percent of sample size. A dash indicates an absent species.
[2]Cover averaged over number of occurrences. 'T' represents trace values of less than 0.5%. A dash indicates an absent species.
[3]Either constancy greater than 45% and characteristic cover greater than 5% or an occurrence with cover greater than 15%.

carinatus, *Quercus garryana-Pseudotsuga menziesii/Elymus glaucus* (blue wildrye), *Quercus garryana/Cynosurus echinatus*, *Quercus garryana-Pseudotsuga menziesii/Festuca ovina* (sheep fescue), and *Quercus garryana-Cercocarpus montanus* (=*C. betuloides*) (birchleaf mountain mahogany). Floristic differences between community types are subtle, due to the widespread prevalence and dominance of naturalized taxa. *Quercus garryana* dominates or codominates with *Pseudotsuga* the overstory and reproductive layers (seedlings and saplings) of these stands. The understory is generally dominated by grasses and forbs with a minor shrub component. Each community type is briefly described below in reference to the information contained in Tables 1, 2, and 3.

The *Quercus garryana/Bromus carinatus* (QUGA/BRCA) community type occurs on flat to convex, mid- and upper-slope positions below 1000 m elevation. This is the driest community type, with an average annual precipitation of less than 640 mm. *Quercus garryana* dominates the

TABLE 2. Estimates of mean and standard deviation ( ) for selected physical, environmental, and soil variables by community type.

	Quercus garryana									
					Pseudotsuga menziesii					
	Bromus carinatus		*Cynosurus echinatus*		*Festuca ovina*		*Elymus glaucus*		*Cercocarpus montanus*	
Number of plots	17		13		10		10		3	
Site variables										
Elevation (m)	667	(159)	596	(176)	607	(313)	484	(150)	702	(215)
Slope (%)	17	(10)	16	(20)	13	(6)	26	(14)	43	(26)
Aspect (deg)[1]	31	(0.27)	162	(0.64)	267	(0.20)	229	(0.50)	146	(0.87)
Annual precip. (mm)[2]	640	(40)	780	(380)	850	(220)	1160	(240)	890	(220)
Dry season precip. (mm)[2]	100	(10)	130	(40)	130	(20)	140	(20)	40	(-)
Soil surface and profile variables										
Rock cover (%)	5	(12)	6	(10)	3	(9)	0.1	(0.3)	0.7	(0.5)
Bare soil cover (%)	0.5	(1)	3	(6)	2	(5)	3	(6)	0	(0)
Litter cover (%)	26	(39)	50	(42)	45	(41)	26	(41)	38	(53)
Litter depth (cm)	1.6	(0.8)	1.2	(0.4)	1.4	(0.7)	1.3	(0.5)	4	(1)
Acidity (pH)[3]	6.5	(0.4)	6.4	(0.4)	6.4	(0.6)	6.1	(0.5)	6.1	(0.5)
Coarse fragments (%)[4]	26	(31)	8	(13)	6	(6)	5	(6)	47	(8)
Depth (cm)[5]	5 to > 40		2 to > 40		13 to > 40		20 to 40		>40	

[1]The estimates for aspect are mean and 'r' which is a measure of concentration about the mean aspect (Batschlet 1981) and has a range of 0 to 1. An 'r' value of 1.0 indicates all measures are identical.

[2]Precipitation values for each plot were interpolated from isohyetalines using annual (Froehlich *et al.* 1982) and dry season, May-September (McNabb *et al.* 1982) precipitation maps.

[3]pH of the first 20 cm of the top mineral horizon.

[4]Percent of first 40 cm of the uphill soil pit surface occupied by coarse fragments (gravel and larger).

[5]Depth expressed only as a range.

overstory. Other overstory species all have less than 35% constancy. The understory is characterized by a sparse shrub layer set in a grass-dominated herbaceous layer. Five of the 11 most common species in the herbaceous layer are grasses. Important herbaceous taxa include *Bromus, Anthriscus scandicina* (bur beakchervil), *Cynosurus, Sanicula graveolens* (sanicle), and *Brodiaea pulchella* (purplehead brodiaea). Common shrubs include *Rhus* and *Ceanothus cuneatus* (wedgeleaf ceanothus).

The *Quercus garryana/Cynosurus echinatus* (QUGA/CYEC) community type occurs at low elevations ($\bar{x}$ = 596 m) on a variety of topographic positions with 780 mm of annual precipitation. *Quercus garryana* dominates the overstory with few other tree species present. *Cynosurus* is the dominant understory species in this type. Two other annuals, *Anthriscus* and *Bromus mollis* (soft brome), are relatively important.

The *Quercus garryana-Pseudotsuga menziesii/ Festuca ovina* (QUGA-PSME/FEOV) community type occurs primarily on valley bottom or toe-slope positions below 1000 m elevation. Annual precipitation (850 mm) is the average for the woodlands we examined. *Quercus garryana* and *Pseudotsuga* codominate the overstory and reproductive layers. The sparse understory is characterized by low cover of *Rhus,* and either *F. ovina,* or *F. occidentalis* (western fescue). Other common taxa include *Cynosurus, Symphoricarpos albus* (white snowberry), and *Osmorhiza chilensis* (sweet cicely).

The *Quercus garryana-Pseudotsuga menziesii/ Elymus glaucus* (QUGA-PSME/ELGL) community type is the most mesic of the types examined, with the highest annual and dry season precipitation (1160 and 140 mm, respectively). This type occurs at the lowest elevations (484 m) of the five community types. The overstory is characterized by an open canopy of *Q. garryana* with occasional *Q. kelloggii. Pseudotsuga* is rarely present in the overstory but small numbers are present consistently in the reproductive layers. The understory contains a patchy and variable cover of *Rhus* and

TABLE 3. Mean and standard deviation ( ) of structural components by community type.

	Quercus garryana									
					Pseudotsuga menziesii					
	Bromus carinatus		*Cynosurus echinatus*		*Festuca ovina*		*Elymus glaucus*		*Cercocarpus montanus*	
Number of plots	17		13		10		10		3	
Physical structure										
Basal area (m^2 ha^{-1})	18	(9)	28	(13)	23	(10)	27	(12)	38	(28)
Height (m)[1]	11	(5)	11	(3)	20	(11)	20	(9)	–	–
Cover by layer										
Tree overstory	37	(18)	40	(17)	41	(14)	44	(9)	68	(20)
Tree reproduction	4	(6)	1	(1)	1	(1)	2	(3)	7	(11)
Tall shrub	6	(8)	5	(7)	5	(5)	11	(14)	0	(0)
Low shrub	6	(11)	3	(10)	2	(4)	0.4	(1)	18	(13)
Herbaceous	41	(18)	43	(15)	32	(16)	45	(14)	48	(36)
Moss and lichen	3	(7)	1	(1)	0.4	(.6)	4	(9)	0.1	(.1)
Average richness by layer[2]										
Tree (total)	2.1	(1.3)	1.9	(1.0)	3.7	(1.6)	3.4	(0.7)	4.3	(1.5)
Tall shrub	1.4	(1.2)	2.3	(1.2)	2.5	(1.1)	1.8	(1.2)	0.0	(0.0)
Low shrub	1.6	(1.5)	0.4	(0.7)	1.3	(1.5)	1.0	(0.8)	1.7	(1.2)
Herbaceous	21.2	(8.5)	12.8	(4.1)	16.6	(6.9)	19.5	(7.6)	17.3	(8.3)
Total	26.5	(8.7)	17.5	(5.5)	24.1	(9.6)	25.7	(8.0)	23.3	(8.0)
Average N_2 diversity by layer[2]										
Tree (total)	1.4	(0.7)	1.1	(0.5)	1.5	(0.6)	1.6	(0.4)	2.0	(0.6)
Tall shrub	1.1	(0.9)	1.3	(0.5)	1.5	(0.6)	1.1	(0.9)	0.0	(0.0)
Low shrub	1.0	(1.0)	0.3	(0.5)	0.9	(0.9)	0.8	(0.6)	1.0	(0.0)
Herbaceous	3.5	(1.6)	3.1	(1.0)	3.7	(2.5)	4.5	(1.3)	2.2	(1.0)
Total	4.4	(1.7)	3.7	(1.7)	4.0	(1.8)	4.9	(1.0)	3.9	(0.4)

[1]Average number of species per 500 m^2 plot. The tree layer includes species in both overstory and reproduction.

[2]Average N_2 diversity per 500 m^2 plot. The tree layer includes species in both overstory and reproduction.

a dense matrix of grasses and forbs. Common herbs and grasses include *Elymus, Cynosurus, Dactylis glomerata* (orchardgrass), and *Anthriscus.*

The *Quercus garryana-Cercocarpus montanus* (QUGA-CEMO) community type is a rare type that appears to be restricted to ridges and rock outcrops at higher elevations ($\bar{x}$ = 702 m) and is restricted to soils on sites with nearly double the coarse fragment content of the other plant community types we describe. Dry season precipitation (40 mm) is the lowest of all community types, although annual precipitation (890 mm) values are average for the five community types. *Quercus garryana* and *Cercocarpus* are the most abundant components of the dense overstory. The understory is typically sparse and patchy. Shrubs are uncommon, except for small amounts of *Rhus.* Typical herbs include *Marah oreganus* (Oregon bigroot), *Daucus pusillus* (rattlesnake weed), *Eriophyllum lanatum* (wooly eriophyllum), and *Galium aparine* (catchweed bedstraw).

Relationships

The eigenvalues of the four axes of the composite ordination, as calculated by DECORANA were (in order) 0.417, 0.158, 0.004, and 0.000 (Figure 3). The relative magnitudes of the axes lead us to interpret only the first two and ignore axes 3 and 4. The first axis separates the QUGA-CEMO community type from the other four types and reflects the floristic differences between this community type and the others. The second axis of the ordination appears to order the community types from relatively moist (low scores) to relatively dry (high scores). The QUGA/BRCA community type,

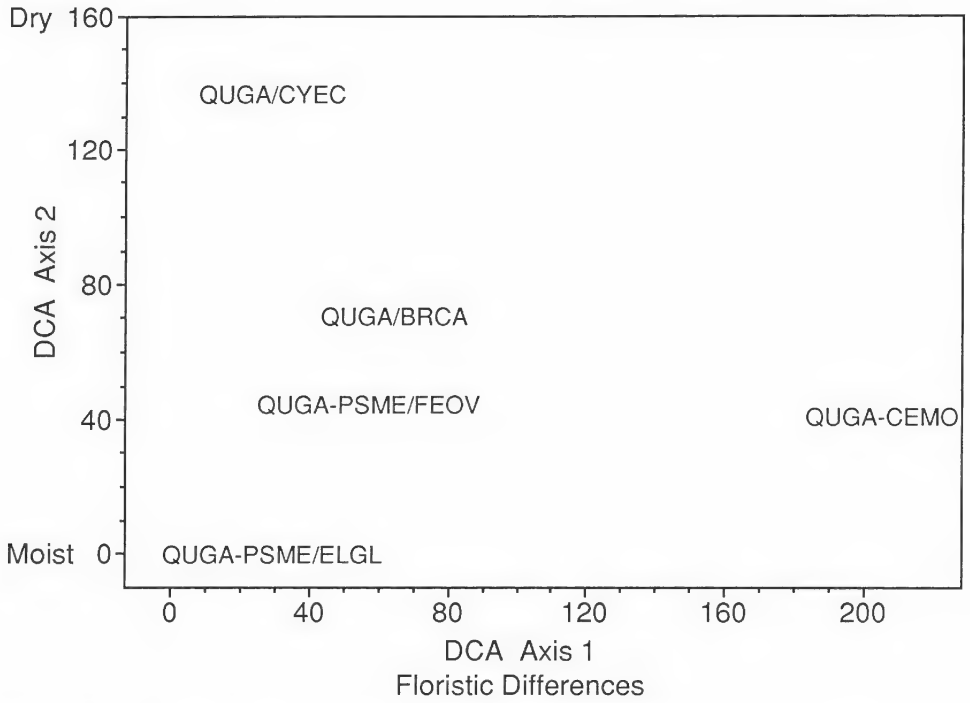

Figure 3. Detrended correspondence analysis (DCA) ordination of composite sample-units. Acronyms for the community types are: QUGA/CYEC, *Quercus garryana/Cynosurus echinatus;* QUGA/BRCA, *Quercus garryana/Bromus carinatus;* QUGA-PSME/FEOV, *Quercus garryana-Pseudotsuga menziesii/Festuca ovina;* QUGA-PSME/ELGL, *Quercus garryana-Pseudotsuga menziesii/Elymus glaucus;* and QUGA-CEMO, *Quercus garryana/Cercocarpus montanus.*

however, does occur in sites with lower precipitation than the QUGA/CYEC type (Figure 3). Results of the rank correlation (Kendall's *tau*) between axis 2 scores and average annual precipitation (γ = 0.8) reinforces this interpretation. To further pursue the role of relative moisture in defining vegetation patterns within these woodlands we rank correlated ordination scores from a data set of original plot data (minus the QUCA-CEMO community type plots) with annual and dry season precipitation values. Correlations with the first axis scores from this ordination were γ = 0.73 and γ = 0.63, respectively.

The similarity matrix (Table 4), also based on composite plot data, illustrates the subtle differences between types, as few strong differences are visible. Only QUGA-CEMO has any dissimilarities with the other types.

TABLE 4. Percentage similarity[1] among composite sample-units for each community type.

	BRCA[2]	CYEC	FEOV	ELGL	CEMO
BRCA	100				
CYEC	59	100			
FEOV	63	49	100		
ELGL	44	41	42	100	
CEMO	48	31	42	28	100

[1]Similarity values were derived using AID-N analysis (Overton *et al.* 1987).

[2]BRCA—*Quercus garryana/Bromus carinatus* community type
CYEC—*Quercus garryana/Cynosurus echinatus* community type
FEOV—*Quercus garryana-Pseudotsuga menziesii/Festuca ovina* community type
ELGL—*Quercus garryana-Pseudotsuga menziesii/Elymus glaucus* community type
CEMO—*Quercus garryana-Cercocarpus montanus* community type

Structure

The four community types influenced by the precipitation gradient show some segregation in productivity. The drier QUGA/BRCA and QUGA/CYEC community types have maximum *Q. garryana* heights of 11 m compared to the mesic QUGA-PSME/FEOV and QUGA-PSME/ELGL types, where heights are closer to 20 m (Table 2). Cover by layer, richness, and diversity show little difference between types. The only marked exception is richness and diversity for the QUGA-CEMO type, which exhibit the lowest values of all types.

Discussion

Precipitation appears to be the key environmental factor governing distribution of *Q. garryana* woodland community types in southwestern Oregon. The significant rank correlations between ordination scores and precipitation values at both the individual plot scale and the community type scale strongly indicate that annual precipitation is a dominant factor in the distribution and composition of these woodlands.

The QUGA/ELGL community type receives the highest overall precipitation, has the highest diversity, and appears to have an understory with the smallest component of naturalized taxa. QUGA/CYEC, the second driest community type, has the largest number of introduced species. This type may represent several historic community types that have lost their distinctiveness due to past disturbances and the presence of highly competitive non-native annual grasses. *Cynosurus echinatus*, a non-native annual grass of low value that thrives in semi-moist soils under oaks, also indicates range deterioration and is common throughout these woodlands (Crampton 1974).

Quercus garryana is considered a climax species on xeric sites (Whittaker 1960, Atzet and Wheeler 1982). A long history of disturbance from livestock grazing, fire suppression, and fuel wood harvest has created an understory currently dominated by non-native annuals. With the dominance of early seral understory taxa, much of which is non-native, differentiating plant associations becomes difficult in an ecosystem that was dominated by late seral and climax perennials.

Relationship to Other Woodlands

Southwestern Oregon *Q. garryana* woodlands ecologically and floristically appear to be transitional from those of the Willamette Valley of northwestern Oregon and the Scott and Shasta valleys of northern California (Griffin 1977). The community types found in southwestern Oregon receiving less than 1000 mm annual precipitation are more like those occurring in northern California. The QUGA-PSME/ELGL type is more similar to Willamette Valley woodland types.

Thilenius (1968) described *Quercus/Rhus* on the most xeric sites in the Willamette Valley, from southern and western aspects of mid to upper slopes (0-20%). *Elymus* and *Cynosurus* were present in the understory. To the southwest, Sugihara *et al.* (1987) describe *Q. garryana* woodlands on Bald Hills in Redwood National Park, northwestern California. They also describe a xeric *Quercus/Cynosurus* community type which occurred on convex, southerly aspects and was the most heavily disturbed by grazing.

Woodlands that are most similar to those found in southwestern Oregon are from the interior valleys of the Umpqua River Basin. Atzet and McCrimmon (1990) describe a *Quercus garryana/Fragaria vesca* var. *bracteata* plant association that occurs on valley floors along the North and South Umpqua Rivers or sites with shallow soils ($\bar{x}$ = 23 cm). Smith (1985) describes *Q. garryana* plant communities from a small area near the North Umpqua River. His apparent strategy was to sample all types regardless of age or disturbance. Several types resemble those found in southwestern Oregon including a *Quercus/Rhus/Taeniatherum asperum* (medusahead)/*Cynosusrus* type and a *Quercus/Rhus/Cynosurus* type. Two other *Quercus* dominated types were also listed but differ from those described above due to a dense shrub layer. These include the *Quercus-Arbutus/Rhus/Cynosurus* type, and the *Quercus/Rhus/Dactylis* type.

Fire, Grazing, and Annual Grasses

Fire suppression is a major factor in the dynamics of these woodlands. Most stands we sampled were even-sized trees with few scattered larger individuals and little regeneration. This is consistent with descriptions by early European settlers that fires were frequent in the valleys, thereby maintaining most valley bottomlands and foothills as grasslands or open savannas (Thilenius 1968). Active fire suppression over the last century has converted open savannas and grasslands to woodlands, and initiated the recruitment of conifers (Thilenius 1968). Atzet and McCrimmon (1990) note that fire

in oak woodlands in the Umpqua River drainages was frequent prior to suppression. These fires burned with low intensity which confined fire to the woodlands, without entering the adjacent dense forested sites.

Fire eliminates conifer seedlings and affects stem density, form, and species composition of the remaining overstory (Plumb and McDonald 1981). Fire also stimulates coppice regeneration of *Q. garryana.* This form of stand regeneration can be more effective than seedling establishment from acorns (Fowells 1965, Sugihara and Reed 1987).

Livestock grazing in these woodlands has influenced the process of change by damaging or destroying oak sprouts, shrubs, and the native grasses which allowed weedy annual grasses to become established. For example, season-long grazing in the Bald Hills of Redwood National Park lowered species richness by reducing the number of kinds of perennials (Saenz and Sawyer 1986). In addition, cattle avoided grazing *Cynosurus,* no doubt aiding its establishment and dominance in these woodlands (Saenz and Sawyer 1986). Decreasing livestock numbers or protecting these woodlands from grazing may cause an increase in the number of perennial grass species with a concurrent decrease in annual grasses (Hektner *et al.* 1983). *Bromus carinatus,* a native perennial which provides good forage, will increase under slight to moderate disturbance but is susceptible to aggressive competition (Crampton 1974). Some nonnative annuals are such strong competitors that even under complete protection from grazing they can maintain dominance.

Early-season grazing may decrease competition for soil moisture and nutrients between annual grasses and oaks. Early growing winter annuals may germinate in the fall and begin utilization of soil resources following adequate precipitation (Matsuda and McBride 1986, Gordon *et al.* 1989). Replacement of native perennial grasses by annual flora shifts the period of soil water utilization from February through July to February through May (Jackson and Roy 1986, Gordon *et al.* 1989). Competition for soil resources, particularly water, shifts from a primarily spatial pattern to a temporal pattern (Welker and Menke 1987). This may cause seedling suppression in drought years and may account, in part, for the decline in *Q. garryana* regeneration (Reed and Sugihara 1987).

Maintenance of *Q. garryana* woodlands in the landscape will require active management. Prescribed burning or thinning is needed to stimulate coppicing and reduce competition with conifers. Grazing management that emphasizes timing of grazing to coincide with phenology of undesirable annual grasses may promote *Quercus* seedling establishment and favor recruitment of perennial grasses. In the bald hills of northwestern California, concern has heightened as many oak woodlands have succeeded to conifers because of fire suppression (Reed and Sugihara 1987). Additional acreage is continually lost to agriculture and suburban development. Without changes in land management a distinctive feature of southern Oregon's landscape will diminish.

Acknowledgments

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Effects of Terrain on Excessive Travel Distance by Snow Avalanches

Abstract

This study was undertaken to determine the characteristics of snow avalanches most likely to travel excessive distances across low-angle runout zones and perhaps onto opposite slopes. "Excessive" travel attained by snow avalanches is related to low equivalent coefficients of friction and large snow volume. In this study, wet-snow avalanches traveling down deeply incised, "hockey-stick profile" avalanche paths exhibited excessive travel. The equivalent coefficients of friction calculated for these avalanches were similar to those determined for far-traveling avalanches elsewhere. Conditions in the runout zone also affect excess travel, because early successional vegetation is less likely to impede continued avalanche travel than a mature forest environment. Large-volume avalanches produce low coefficients of friction resulting in excessive travel into the low-angle portions of the runout zones where erosion is possible. Land-use planners can utilize these observations in identifying particularly hazardous sites.

Introduction

Mass movements of snow, rock, or weathered surficial debris occasionally flow excessive distances across the landscape, owing to low coefficients of friction and large volumes. In the context of snow avalanches, "excessive" distance can be considered either from a planning perspective, i.e., in excess of the 100-year avalanche runout zone (Ives *et al.* 1976); or in a physically based context, i.e., in excess of normal travel distances given certain terrain parameters (Izumi 1988, Yamada 1989). The latter approach has also been applied in studies of rockfall-avalanches (sturzstroms) (Hsü 1975, Eisbacher 1979) and volcanic debris flows (lahars) (Naranjo and Francis 1987). The distances traveled by such mass movements are indicative of the fundamental physical processes operating on, and influenced by, the landscape.

Snow avalanches in subalpine terrain typically occur within well-delineated paths which pass vertically through the surrounding forested environment, producing distinct swaths of non-forested, supple vegetation (Malanson and Butler 1984, 1986; Butler 1989a; Erschbamer 1989). The transverse and longitudinal boundaries of these avalanche paths mark the zone within which the geomorphic influence of a snow avalanche is typically confined. However, infrequent high-magnitude snow avalanches can extend beyond the longitudinal and transverse margins of the path and into the surrounding forest, uprooting trees and introducing sediment into the slope debris cascade (Butler 1989a, Butler and Malanson 1990). Because these infrequent, spatially extensive avalanches are erosionally active in normally unaffected portions of paths, an understanding of the type and characteristics of avalanches which travel excessive distances is important from both a geomorphic and planning perspective.

The purposes of this paper are to: 1) examine the terrain and avalanche characteristics associated with historical cases of snow avalanches which possessed large volumes, low coefficients of friction, and therefore excessive travel distances in a portion of the northern Rocky Mountains of Montana, U.S.A.; and 2) describe historical cases in which no excessive travel occurred. We compare our results with those from studies in other mountain environments with generally similar avalanche climates.

Background

Excessive travel distance by a snow avalanche is a function of a number of factors: type of avalanche, snow conditions, vegetation encountered along the avalanche track and in the runout-zone, climate, terrain relief, and morphology of the avalanche path (Mears 1979, 1984). It has been held that wet-snow avalanches and avalanches comprising large blocks derived from the fracture of a hard, dry snow slab develop large internal frictional forces among the moving blocks, the avalanche, and the path surface (Mears 1984, p. 82). These large frictional forces cause rapid deceleration in

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the runout zone and relatively short runout distances. Conversely, dry-snow powder avalanches entrain air, become partly fluidized into diffuse aerosols, and possess small internal frictional forces, resulting in dispersal of the avalanche deposit over long distances at the base of the slope. Deceleration and reduced dispersal may result from encountering wet or blocky snow in the travel path, or from interacting with large trees and understory vegetation which dissipate energy quickly (Mears 1984).

Recently, Martinelli (1986), Izumi (1988), Mears (1988, 1989), and McClung *et al.* (1989) have reviewed empirical snow-avalanche runout models based on analysis of terrain variables, particularly those developed by personnel at the Norwegian Geotechnical Institute. Mears (1988, 1989) and McClung *et al.* (1989) examined data on runout distances from four different geographic areas, and demonstrated that the Norwegian approach is not applicable to many of the climates and terrains that produce avalanches in North America. They concluded that the statistical runout equations developed in one mountain area should not be applied to other areas.

Mears (1988) also pointed out a basic problem with physical models for calculating avalanche runout distance: they are dependent on the use of a friction-term value (the coefficient of friction) which varies with terrain and snow type, and which have not been measured. The values for the coefficient of friction are typically estimated, based on the experience of the user. Commonly used values range from 0.1 to 0.5 (Buser and Frutiger 1980, Perla *et al.* 1980).

In the statistical models developed by others and discussed and used by Mears (1988 p. 233, 1989 p. 284) and McClung *et al.* (1989), the vertical relief of the avalanche path (H), has been identified as an important controlling variable (Figure 1). However, because a snow avalanche is not always initiated at the top of the avalanche path, but at some lower elevation, it is more useful to define H as the vertical relief from the top of the breakaway scar. This redefinition of H was earlier employed by Hsü (1975), Eisbacher (1979), and Naranjo and Francis (1987) in their examination of excessive travel distances of sturzstroms and lahars. This approach has also been used in Japanese (Izumi 1988; Yamada 1989) and Norwegian

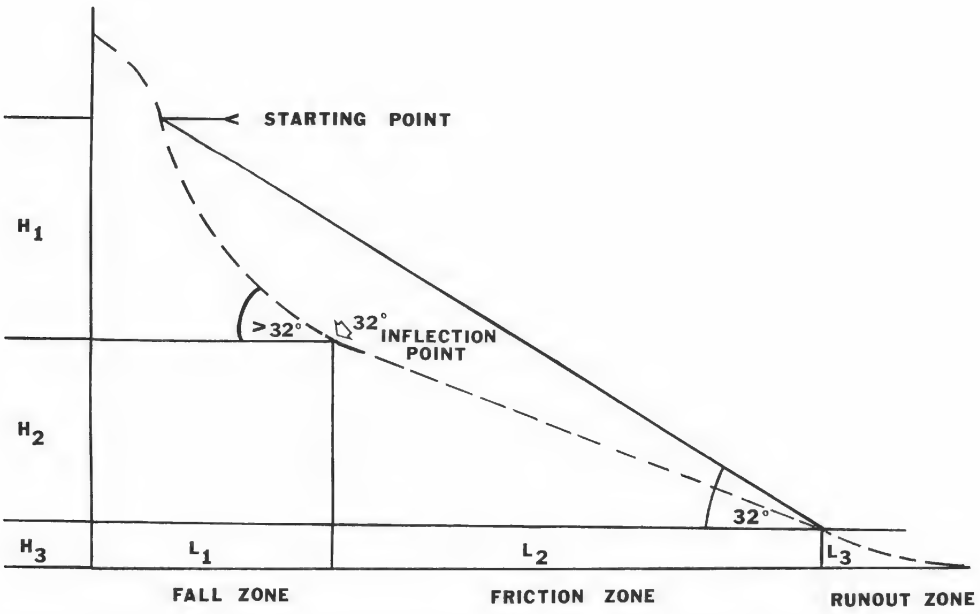

Figure 1. Longitudinal profile of typical snow-avalanche path, with key points and zones as discussed in text. H, height; L, length; dashed line represents hypothetical longitudinal profile of avalanche path.

(Lied and Bakkehøi 1980) studies of snow-avalanche excessive travel distances.

Glenne (1986) and Izumi (1988) defined H as "the vertical avalanche fall height," rather than as the total relief of the avalanche path, and L as the horizontal reach of the avalanche (Figure 1). With these variables, they subsequently calculated the equivalent coefficient of friction (μ) as:

$$\mu = H/L. \quad (1)$$

Excessive travel distance (Le), defined by Hsü (1975, p. 138) as "the horizontal displacement of the tip. . . beyond the distance one expects from a frictional slide down an incline with a normal coefficient of friction of tan 32° (0.62)," may be expressed as:

$$Le = L - H/\tan 32°. \quad (2)$$

The 32° angle, typically utilized in sturzstrom work, has also been experimentally confirmed by Japanese workers for use with snow avalanches (Izumi 1988).

Izumi (1988) utilized Hsü's (1975) definition in a modified form, referring to an "unlubricated slide mass" rather than a "frictional slide." Although Izumi used the term "slide mass," it is assumed that avalanche motion is not necessarily a sliding one, but in all likelihood a turbulent flow (a point emphasized by Glenne, 1986). Izumi illustrated an inverse relationship between avalanche volume and equivalent coefficient of friction, and a direct relationship between volume and excessive travel distance.

Izumi's (1988) results from the study of both wet- and dry-snow avalanches in the maritime mountains of Japan therefore illustrated relationships similar to those from sturzstrom and debris avalanche studies: mass-movements having greater volumes tended to exhibit lower equivalent coefficients of friction, and were more likely to travel long distances. Slab avalanches of dry snow had the lowest coefficients of friction in Izumi's study, and as a group the slab avalanches also had the greatest excessive travel distances. Full depth, dry powder avalanches had intermediate coefficients of friction generally in the range of 0.4 to 0.6; and full depth, wet-snow avalanches had the highest μ values, ranging from 0.4 in one case to the more typical 0.6 to 0.8 range. Excessive travel distance for the dry, full-depth avalanches was limited, typically less than 200 m. Only one wet snow avalanche achieved excessive travel distance. All slab avalanches in Izumi's sample traveled excessive distances, ranging from 100 to 1,800 m.

In review, two aspects of the work on avalanche distances need to be reiterated. First, the concept of "excessive distance" is very important. Mears (1989) referred to "maximum runout distance" of a "design avalanche." His calculation of a runout ratio expressed the concept of excessive distance, and McClung and Lied (1987) and McClung *et al.* (1989) have shown how this concept can be used in a predictive method. Hsü (1975) and Izumi (1988) specified a precise definition of "excessive" as in excess of an expected distance, which itself needs further consideration. For Mears' (1989) formula for runout ratio (RR), it is necessary to measure the horizontal component of path length above and below a 10° slope angle on the path (10° being the presumed angle below which retardation of snow motion occurs; Lied and Bakkehøi 1980). In Hsü's (1975) formula (equation 2), excess length is the total actual length minus the expected length, which in turn is equal to the horizontal length defined by a straight line of 32° slope originating at the top of the slide. It should be noted that the process of locating either of these tangents to the slope may produce error or bias depending on the scale of the source material, whether topographic maps, aerial photographs, or digital elevation models (Walsh *et al.* 1987).

Both definitions embody valuable concepts. In Mears (1989) we find that the excessive distance is a function of the length of a runout zone relative to an upper path or slide zone. For Hsü (1975), the distinction between the two is less arbitrary, with the 32° figure being based on observational and experimental results for sturzstroms, which may be cautiously applied to snow avalanches. Izumi's (1988) "equivalent coefficient of friction" has value as an easily calculated index not requiring overly precise (i.e., larger than 1:24,000-scale) topographic maps or time-consuming field data collection.

Other factors influencing excessive runout are the topographic features of the path itself and the terrain in which the path is located. Runout distance is not affected by conditions in the starting zone, for either a dry or wet-snow avalanche, on unconfined avalanche paths. The angular transition between track and runout zone is significant for identifying paths with the potential for extremely long runout distances (Martinelli 1986, p. 30). Avalanche paths having linear or slightly concave

tracks with abrupt transitions (at point L3 on Figure 1) to nearly flat runout zones have been called "hockey-stick paths" by Martinelli (1986), and avalanches on such paths have tended to run "unusually long distances." The transverse profile across an avalanche path is an important morphological variable that has not been incorporated into mathematical runout models, and should be. On confined (channelized) avalanche paths, released snow is forced through a confined track, therefore increasing velocity and making runout distance dependent on the size of the starting zone, i.e., making runout distance dependent on snow volume (Mears 1979). A recent paper by Nicoletti and Sorriso-Valvo (1991) illustrates how transverse morphologic controls can be incorporated into computations of runout distance for rock avalanche, and offers promise for similar applications in snow-avalanche runout prediction.

The Study Area

Glacier National Park (GNP) is located in northwestern Montana, U.S.A., astride the continental divide. The western half of GNP (Figure 2) has a modified Pacific maritime climate with relatively mild temperatures and heavy, wet snowfall. East of the divide, winters are much colder and windier, and snowfall tends to be drier and light. Pleistocene glaciation produced a steep landscape prone to snow avalanches, and Butler and Malanson (1985a) and Butler (1986a) have illustrated the geographically-widespread occurrences of avalanches in GNP, the types of avalanches that occur, and the climatic conditions that produce them. Slab and point avalanches of wet and dry powder snow have been reported from both sides of the continental divide.

Figure 2. Location of historical snow avalanches discussed in the text. 1, Goat Lick 1979 and 1982 avalanches. 2, Shed 7. 3, Mt. Henkel. 4, Josephine Lake. 5, Kintla Lake.

Analysis

Six cases (Figure 2) of snow avalanches of known type, and with known initiation and termination elevations, are available in published and archival literature from GNP (Anonymous 1946, *Hungry Horse News* 1975, Panebaker 1982, Martinelli 1984, Williams and Armstrong 1984, Butler and Malanson 1985b, Frauson 1979). Data on the volumes of these avalanche deposits were not measured, but can in some cases be reconstructed from the areal extent of avalanche deposits visible on photos, in combination with depth estimates derived from evidence of vegetation damage along path margins.

For each of the six historic cases, H was calculated by subtracting the lowest elevation of the avalanche deposit from the highest known starting elevation. L was calculated by mapping the location of the snow failure zone and the avalanche deposit on U.S.G.S. 1: 24,000-scale topographic maps and measuring the horizontal distance down the center of the path between the upper and lower elevations. Distance measurements are therefore considered accurate to within 20 m. The equivalent coefficient of friction for each case was calculated using equation 1 (Table 1). Le was calculated for each case using equation 2. By comparing Le to μ, we examine the length of an avalanche in terms of its average slope and a slope of 32°. For lower average slopes, i.e., lower coefficients of friction, the distance in excess of a 32° run will be greater for a given path length.

Table 1 also provides information on avalanche characteristics and path terrain. The type of avalanche is recorded for each example. Volume of the snow deposited in the runout zone was estimated in the cases of the Goat Lick (1979 and 1982) and Shed Seven avalanches by mapping the areal extent apparent on photographs in Panebaker (1982), Martinelli (1984), and Williams and Armstrong (1984); and by estimating snow depth either from the known height of objects in the photographs, or from the height of vegetation in the runout zone (Butler and Malanson 1985b). Terrain conditions and type of vegetation within each avalanche path's track and runout zone were examined in the field (Figures 3, 4) for all but the

TABLE 1. Calculation of equivalent coefficient of friction and excessive travel distance for six snow avalanches, Glacier National Park

Path Name	V[1]	H	L	H/L	L_e	Type Avalanche
Goat Lick 1979	2.67	975.4	2529.8	.386	969.0	Wet snow in steep, narrow gully
Goat Lick 1982	1.27	1127.8	2529.8	.446	877.6	Wet snow in steep, narrow gully
Shed 7 1979	0.86	737.6	1724.6	.428	544.1	Wet snow in steep, narrow gully
Mt. Henkel 1979	n.a.	1036.2	2377.4	.436	719.0	Wet snow (with wind?) in steep, narrow gully
Josephine Lake 1975	n.a.	646.2	731.5	.883	−310.8	Dry powder with wind on open slope
Kintla Lake 1946	n.a.	1544.5	2255.5	.685	−235.6	Dry powder with wind in steep, narrow gully

[1]Volume, in $10^5 m^3$.

n.a., not available.

Figure 3. Inner zone of steeply plunging Goat Lick avalanche path.

Figure 4. Shed 7 avalanche path, with deeply incised central gully and low, herbaceious vegetation (arrow). Furthest reaches of the runout zone in foreground. Note the snowshed covering the railroad tracks.

Kintla Lake case, which was studied using aerial photographs and a topographic map. Factors particularly affecting the potential for excessive runout were the degree of incision (if any) of a central channel running longitudinally down the path (the "inner zone"), the longitudinal profile of the path (*sensu* Martinelli 1986), and the character of vegetation present, categorized as: inner zone, of primarily herbaceous vegetation such as *Urtica dioica;* flanking zone, of flexible deciduous trees such as *Alnus sinuata, Acer glabrum,* and *Populus tremuloides;* and outer zone, of more widely scattered trees and shrubs such as *Amelanchier alnifolia* (Malanson and Butler 1984, 1986).

Results

Each of the snow-avalanche paths examined has a "hockey-stick path profile" (Martinelli 1986), a steeply plunging upper track with a pronounced break in slope leading to the low-angle runout zone. Of the six cases examined (Table 1), four avalanches possessed relatively low equivalent coefficients of friction (<0.5) compared to those avalanches in this study and Izumi's (1988) which did not travel excess distances. The four avalanches with lower equivalent coefficients of friction attained excessive travel distances of 544-969 m. Volumes exceeded 85,000 (0.85×10^5) m^3 in the three cases for which reconstruction of depositional volume was possible.

These data compare favorably with Izumi's (1988) results. He illustrated that avalanches larger than 1×10^5 m^3 experienced excessive travel distance. However, all such avalanches in his sample were slab avalanches of dry snow. The wet-snow avalanches he examined rarely exceeded 0.3×10^5 m^3 in volume, and thus uniformly high equivalent coefficients of friction (> 0.58 in all but one case) and did not experience excessive travel.

In contrast to Izumi's (1988) findings, all avalanches in our study which possessed low coefficients of friction and excessive travel distance were wet-snow avalanches. The Glacier Park wet-snow

avalanches occurred in deeply-incised, steeply plunging paths with well-defined inner zones of low herbaceous vegetation (Figure 3). These conditions apparently precluded significant energy dissipation along the lateral margins of flow, so that the low friction and continued high energy levels favored excessive travel in the runout zone. A similar conclusion for rock avalanches was recently reported by Nicoletti and Sorriso-Valvo (1991).

The transverse shape of an avalanche path also seems to be important. A dry-snow avalanche incorporating air can have considerable depth so the relative proportion of the avalanche contacting the ground will be small, even on a flat slope. In wet-snow avalanches, however, this ratio of volume to contact will be low unless the flow is channelized by local terrain features.

Conditions in the runout zone in each case of excessive travel also favored continued movement. In the two Goat Lick avalanches, the snow discharged onto the floodplain of the Middle Fork of the Flathead River, where vegetation is sparse to non-existent. The Shed 7 avalanche encountered young conifers where power line maintenance had removed the mature vegetation (Figure 4); and the Mt. Henkel avalanche debouched into a post-fire successional grove of young aspen (*Populus tremuloides*).

The two avalanches which did not experience excessive travel had high equivalent coefficients of friction (Table 1), in the same range as those described by Izumi (1988) which did not undergo excessive travel. Both our cases involved dry-powder avalanches with accompanying windblast. The Josephine Lake avalanche (Table 1) occurred on an open, unconfined slope, i.e., it did not travel down a deeply incised gully in the center of the avalanche path. The lack of confinement in a central gully may allow energy to dissipate along an avalanche's lateral margin, leading to an increase in friction and a shorter travel distance. Although volume information was not available for this avalanche, it possessed sufficient strength to demolish a boat-storage shed at the base of the path, possibly a result of the associated windblast (*Hungry Horse News* 28 February 1975).

The other case of avalanching without excessive travel, at Kintla Lake (Table 1), did occur on a path with the requisite terrain conditions for excessive travel; a steeply plunging and deeply incised central gully with low herbaceous vegetation in the inner zone. However, the low-angle runout zone was limited in extent, and the avalanche entered a mature coniferous forest near the head of that zone (Anonymous 1946). Entry into the forest, causing increased friction during flow plus uprooting and destruction of the trees, dissipated the energy that might otherwise have propelled the avalanche farther into the runout zone.

Discussion

The number of avalanches examined in this study is low, mainly because of the limited number of on-site observations of starting elevation. However, tree-ring data reveal that far-traveled avalanches also reached the longitudinal peripheries of the Goat Lick path in the winters of 1971-72, 1964-65, 1962-63, 1956-57, 1949-50, 1944-45, 1936-37, 1934-35, and 1924-25 (Butler and Malanson 1985a); and that avalanches reached the outer edges of the Shed Seven runout zone in the winters of 1975-76, 1973-74, 1971-72, and 1968-69. Frauson (1979) also described another snow avalanche with excessive travel distance at the Mt. Henkel path, also occurring in 1979; unfortunately, no data were available concerning starting elevation. These additional examples reveal that snow avalanches frequently have traveled long distances in Glacier Park.

Rainfall associated with a rise in temperature is the most common climatic trigger of snow avalanches in GNP, and wet-snow avalanches are the most common type (Butler 1986a). Historical data corroborate that most cases of excessive travel at the Goat Lick and Shed Seven paths were wet-snow avalanches (see Butler 1986b, for details).

Given the results of this and other studies, a general model of avalanche movement and energy is desirable. We propose some directions for such a task that can be easily applied by land-use planners without intensive labor requirements associated with on-site monitoring. In Figure 1, we show the longitudinal profile of a typical avalanche path, with several key locations noted. The path is divided into three portions: the part 32° and steeper (Izumi 1988) (H1 and L1); the part below that point but above the point defined by an average 32° slope (H2 and L2); and the runout zone (H3 and L3). We can refer to these as the fall zone, the friction zone, and the runout zone. The motion of an avalanche will be generated during the fall on the slope steeper than 32°; this

energy will mostly be dissipated in the friction zone; and the extent to which it is not fully dissipated in the friction zone will be expressed in the length of the runout zone. Thus excessive distance is, as expressed by McClung and Lied (1984, 1987) and Mears (1989), a function of the ratio of the lengths of two portions of the path. We suggest, however, that it is the upper two sections of the path that are important in determining the excessive distance traveled (that distance which exceeds the calculated value for an average slope of 32°). The excessive distance is, then, a direct function of H1, and an indirect function of H2. Also, the coefficients of the function(s) may differ for the portions of the slope above and below H2. The exact function need not be specified here because, as noted in most studies, other factors must also be taken into account.

Glenne (1986) summarized many of these factors relative to a smooth longitudinal surface: they include weather and snowpack, melting, and the changes in mass of the avalanche along the path (the friction of moving snow is also a function of its mass and volume). We have emphasized the importance of local terrain and vegetation. We note that the transverse topography and vegetation of a path may affect the friction, because of changes in the area of surface contact relative to the mass and volume of the avalanche. Variation in the longitudinal topography and vegetation, beyond the effects of a large stand of trees at the bottom of a slide, must also be considered. For example, our Shed 7 path, and many others in Glacier Park, the Rocky Mountains in general, and in Europe, pass over a snowshed (gallery) which will cause a fast-moving flow to become airborne for at least a short distance. Abrupt profile interruptions to a generally concave "hockey-stick" profile could also cause snow acceleration or deceleration, depending on the shape (convex or concave) and steepness of the interruptions.

Conclusions

Our data reveal that many wet-snow avalanches can travel excessive distances with low equivalent coefficients of friction. Our data do not preclude the possibilities that slab and dry-snow avalanches may also travel excessive distances, as described by Izumi (1988) and Yamada (1989) for Japanese avalanches; however, our limited historical sample reveals no such cases. In the northern Rocky Mountains, excessive travel distances develop where large-volume avalanches are released on "hockey-stick profile" paths which are deeply incised. A flume-like terrain works in concert with low-stature, flexible vegetation of the inner zone to provide minimal frictional resistance to the passage of the snow; and movement continues into low-angle runout zones where vegetation is limited in areal extent and height. Where avalanches do not travel in confined paths, and/or where they encounter mature forest in the runout zone, excessive travel is unlikely.

These findings have several geomorphic implications. Effective scouring of the below-snow surface will be limited to the transverse (Butler and Malanson 1985a, Butler 1989a) and distal margins of avalanche paths. Inner zones of steeply plunging avalanche paths subject primarily to wet-snow avalanches are not likely to experience significant avalanche erosion. As pointed out elsewhere (Butler and Malanson 1990), these flume-like snow-avalanche paths seem to be relict landforms.

In the outer margins of avalanche runout zones, forest may be entered and trees uprooted (Butler and Malanson 1990). Deposition of dense wet-snow avalanches can also block creeks and rivers, producing temporary dams which ultimately fail and release jokulhlaup-like outburst floods of surprisingly high peak discharges (Butler 1989b).

Land-use planners can utilize the information presented in this paper to identify particularly dangerous sites. Excessive travel likelihood can be quickly calculated by determining the equivalent coefficient of friction using $\mu = H/L$. The necessary data for such calculations are quickly and easily extracted from topographic maps and maps of avalanche path location (Butler and Walsh 1990), in concert with descriptions of past avalanches. Even if historical data are absent, runout zones and slopes opposite avalanche paths that are most likely to be impacted by excessive travel can be identified on the basis of path topography; "hockey-stick profile" paths (easily discernible from topographic maps) with deeply incised central gullies (also easily identified on maps) present the greatest danger. Limiting development on, immediately across from, and downvalley from such paths seems the most prudent course for planners seeking to apply our observations.

Acknowledgements

We thank officials of Glacier National Park for access to archival data, the University of Georgia for financial support, Stephen J. Walsh for field collaboration, and the logistical support of Freda's, West Glacier.

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ERRATUM

The attention of readers is drawn to the following correction in the article by R. G. Hein, J. L. Musser, and E. F. Bracken "Serologic, Parasitic and Pregnancy Survey of the Colockum Elk Herd in Washington."

Correction volume 65, number 5, page 219, column 1, paragraph 4; recycling of the narcotics was *not* observed as originally reported.

A Joint Meeting

Northwest Scientific Association

— 65th Annual Meeting —

Society for Northwestern Vertebrate Biology

Northwest Lichen Guild

American Fisheries Society *

March 24-28, 1992
Western Washington University
Bellingham, Washington

PROGRAM and ABSTRACTS

*Program printed separately

SCHEDULE OF EVENTS

Tuesday, March 24		
7:00 P.M. - 9:00 P.M.	Reception/ Registration	Canada House
8:00 P.M. - 10:00 P.M.	NWSA Board Meeting	Bond Hall 151
Wednesday, March 25		
8:00 A.M. - 12:00 noon	Registration	OM Reg. Center
8:30 A.M. - 12:00 noon	Biodiversity Symposium	Lecture Hall 2
10:20 A.M. - 12:00 noon	Marine Biol	Bond Hall 103
12:00 noon - 1:30 P.M.	Luncheon	Viking Commons
1:30 P.M. - 5:00 P.M.	Biodiversity Symposium	Lecture Hall 2
1:30 P.M. - 5:00 P.M.	NWSA Sessions	
	Marine Biol	Bond Hall 103
	Geol/Biol	Bond Hall 111
7:00 P.M. - 9:00 P.M.	Nature Seminar	Bond Hall 109
Thursday, March 26		
8:00 A.M. - 12:00 noon	Registration	OM Reg. Center
8:30 A.M. - 12:00 noon	NWSA Sessions	
	Botany	Bond Hall 106
	Forestry	Bond Hall 112
	Zoo/Aquatic	Bond Hall 111
12:00 noon - 1:30 P.M.	Luncheon and Business mting	Viking Commons
1:30 P.M. - 5:00 P.M.	NWSA Sessions	
	Forestry	Bond Hall 112
	Lichens	Bond Hall 103
	Vert. Zool	Bond Hall 106

SCHEDULE OF EVENTS continued

Thursday, March 26		
5:30 P.M. - 6:30 P.M.	Reception	Viking Lounge
6:30 P.M. - 9:00 P.M.	Banquet	Viking Lounge
Friday, March 27		
8:00 A.M. - 12:00 noon	NWSA Sessions	
	Botany	Bond Hall 106
	Lichens	Bond Hall 103
	Vert. Zool	Bond Hall 112
12:00 noon - 1:30 P.M.	Luncheon	Yer on yer own
1:30 P.M. - 5:00 P.M.	Hypogymnia Workshop	Haggard Hall 331
1:30 P.M. - 5:00 P.M.	Wetlands Symposium	Lecture Hall 2
Saturday, March 28	**Field Trips**	Haggard Hall
Skagit wetlands/ Padilla Bay		9:00 A.M.-4:00 P.M.
Sulfur Creek - Lichens & Mosses		8:00 A.M.-5:00 P.M.
Noisy Creek - Old growth forest		8:00 A.M.-5:00 P.M.

BIODIVERSITY SYMPOSIUM
March 25, 1992, Lecture Hall 2

Moderator: **John Miles**, Dean
Huxley College of Environmental Studies
Western Washington University

8:30 - 9:00 **Elliot Marks.** Biodiversity at risk: saving all the pieces. **(abstract #)**

9:00 - 9:40 **David L. Peterson.** Landscape management in a changing environment. **(1)**

9:40 - 10:20 **Ross Kiester.** Biological diversity and forest management: a look to the future. **(2)**

10:00 - 10:40 Coffee break

10:40 - 11:20 **Jim Lichatowich.** Status and importance of stocks in the Pacific salmon resource. **(3)**

11:20 - 12:00 **James W. Vincent.** Economics of biodiversity: market values. **(4)**

12:00 noon - 1:30 Luncheon, Viking Union Commons

1:30 - 2:10 **Daniel A. Hagen.** The economics of biodiversity: non-market values. **(5)**

2:10 - 2:50 **Ed Schreiner.** A National Park Service perspective on biodiversity. **(6)**

2:50 - 3:10 Coffee break

3:10 - 3:50 **Mark Sheehan.** Washington Department of Natural Resources' strategy for the protection of biodiversity. **(7)**

3:50 - 4:30 **Peter T. Haug.** Conserving biodiversity at the landscape level: choices in the managed forest. **(8)**

4:30 - 5:00 Overall questions and answers

WETLANDS SYMPOSIUM

March 27, 1992. 1:30 - 5:00 P.M.

Moderator: **David T. Mason**
Fairhaven College
Western Washington University

There is a growing need for effective **indexes of wetlands functions.** Available tools are expensive, cumbersome, and consequently, exclude direct citizen involvement. This symposium will explore new and traditional techniques for assessing wetlands functions, techniques that probe the complex interactive wetland environment within relative ease, moderate-to-low expense, and which may provide meaningful site-specific data for decision-makers.

PARTICIPANTS - Panelists will informally discuss their own works as well as comment on each others' ideas in a search for effective indicators of wetlands functions.

Jay Zedler: Saltmarsh ecologist and restorationist. California State University at San Diego.

Gary Williams: Wetlands functions and values. Consultant, Vancouver B.C.

Ron Thom: Northwest saline wetlands functions. Battell Marine Science Labs, Sequim, WA.

Charles Simenstad: Wetlands classification. Fisheries Research Institute, Univ. of Washington.

Buddy Clairain, Jr.: Wetlands function modeling. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS.

David Mason: Stress-strain models of saltmarsh, plankton, and benthic community functions in arctic saltmarshes and San Francisco Bay. Fairhaven College, WWU.

GEOLOGY/GENERAL BIOLOGY

Wednesday afternoon, 25 March, Bond Hall 111
Presiding: **Gerald Kraft**, Western Washington University

1:30 MARS AFTER VIKING: POSSIBILITIES FOR LIFE. **David J. Thomas**, Central Washington University and **Joshua P. Schimel**, Institute of Arctic Biology. **(9)**

1:50 THE NOAA NATIONAL BENTHIC SURVEILLANCE PROGRAM DATA BASE. **John T. Landahl**, Environmental Conservation Division, NMFS, NOAA, Seattle, WA. **(110)**

2:10 THE DISPOSAL OF HOUSEHOLD HAZARDOUS WASTE: RESULTS FROM A SURVEY OF PIERCE COUNTY, WASHINGTON. **David A. Swanson**, Center for Social Research, Pacific Lutheran University, Tacoma, WA. **(10)**

2:30 ALKALI LAKE, OR: GEOLOGY OF A TOXIC WASTE SITE. **Kenneth A. Cameron**, Geologist, Oregon Department of Environmental Quality. **(11)**

2:50 - 3:20 Coffee break

3:20 PRELIMINARY INVESTIGATION OF GARDNER CAVE, PEND OREILLE COUNTY, WASHINGTON. **Eugene P. Kiver, John P. Buchanan, Brenda R. Gibson, William A. Graham, Iain A. Olness, and Richard Severn**, Eastern Washington University. **(12)**

3:40 THE NOVEMBER 1990 FLOOD IN SOUTH WESTERN BRITISH COLUMBIA, AN OVERVIEW OF THE RESTORATION PROCESS. **C. Robert Bland** and **P. Eng.** **(13)**

4:00 HYDROLOGIC SIMULATION OF THE LAKE WHATCOM WATERSHED. **Steven J. Walker**, Institute for Watershed Studies, Huxley College, Western Washington University, **(14)**

4:20 EFFECTS OF CYST DENSITY AND AGE ON THE SEDIMENTATION OF GIARDIA CYSTS. **Eniko A. Kramar**, Central Washington University. **(15)**

MARINE BIOLOGY

Session 1 - Wednesday morning, 25 March, Bond Hall 103
Presiding: **Steve Sulkin**, Shannon Point Marine Center

10:20 ENVIRONMENTAL CUES AND THE REPRODUCTIVE CYCLES OF THREE TEMPERATE ASCIDIAN SPECIES. **Brian L. Bingham**, Shannon Point Marine Center, Anacortes, WA. **(16)**

10:40 THE DEVELOPMENT AND PHYSIOLOGICAL RESPONSE OF CANCER MAGISTER MEGALOPAE TO DUEL CYCLES OF TEMPERATURE AND SALINITY. **Matthew W. Johnson**, Western Washington University. **(17)**

11:00 NUTRITIONAL ANALYSIS AND EFFECT OF CRUDE OIL ON THE LARVAL DEVELOPMENT OF HEMIGRAPSUS OREGONENSIS. **Mary Jo Hartmen**, Western Washington University. **(18)**

11:20 GROWTH OF THE RED TIDE ALGA HETEROSIGMA AKASHIWO. **Chris N. Fairbanks**, Western Washington University. **(19)**

11:40 CLAM SPECIES AND VERTICAL DISTRIBUTION ON A COARSE AND FINE SEDIMENT BEACH IN PUGET SOUND, WASHINGTON. **Douglas P. Hanson**, Central Washington University. **(20)**

12:00 noon - 1:30 Luncheon, Viking Union Commons

Session 2 - Wednesday afternoon, March 25, Bond Hall 103
Presiding: **Steve Sulkin**, Shannon Point Marine Center

1:30 THE SPAWNING DYNAMICS OF WALLEYE POLLOCK, THERAGRA CHALCOGRAMMA IN SHELIKOF STRAIT, GULF OF ALASKA. **Nazuka Merati**, NOAA-Fisheries, Seattle, WA. **(21)**

1:50 RNA/DNA RATIOS AS INDICATORS OF NUTRITIONAL CONDITION OF LARVAL WALLEYE POLLOCK, THERAGRA CHALCOGRAMMA. **Michael F. Canino** and **Kevin M. Bailey**, Alaska Fisheries Science Center, NOAA, Seattle. **(22)**

2:10 MANAGEMENT ADVICE FROM A SIMPLE DYNAMIC POOL MODEL WHEN STOCK-RECRUITMENT PARAMETERS ARE UNCERTAIN. **Grant Thompson**, National Marine Fisheries Service, Seattle, WA. **(23)**

2:30 EFFECTS OF UVBR ON SURVIVAL OF MEDAKA EMBRYOS. **Andrea J. La Tier** and **Jack Hardy**. Huxley College, Western Washington University. **(24)**

2:50 - 3:20 Coffee break

3:20 DISTRIBUTION AND SUMMER STANDING CROP OF SEAGRASSES AND MACROALGAE IN PADILLA BAY, WASHINGTON, 1989. **Douglas A. Bulthuis**, Padilla Bay National Estuarine Research Reserve, Washington Dept. Ecology, Mount Vernon, WA. **(25)**

3:40 Title to be announced - **Bill Gardiner**

4:00 HOW DIFFERENT ARE SAND DOLLARS? AN EXAMINATION OF THE ORAL-SURFACE PODIA AND SIEVE HYPOTHESES IN DENDRASTER EXCENTRICUS. **Don C. Williams**, Western Washington University. **(26)**

4:20 DELAYED HATCHING OF SQUID AS A RESULT OF REDUCED LIGHT LEVEL. **William C. Summers**, Western Washington University. **(27)**

UNDERSTANDING NATURE THROUGH ART
Wednesday evening presentation, March 25, 7-9 P.M.
by **Tony Angell**

ZOOLOGY/AQUATIC BIOLOGY

Thursday morning, 26 March, Bond Hall 111
Presiding: **Gerald Kraft**, Western Washington University

8:30 PHONOTACTIC RESPONSE IN ORTHOPTERANS: SYLLABLE DISCRIMINATION OF FEMALES IN THE CALLING SONG OF MALE HOUSE CRICKETS, ACHETA DOMESTICUS. **Gary D. Lorenson**, Central Washington University. **(28)**

8:50 AN EVALUATION OF ASSOCIATIONS BETWEEN MACROINVERTEBRATES AND MACROPHYTES IN CANNERY POND. **Jenifer K. Parsons**, Western Washington University. **(29)**

9:10 JUVENILE ONCORHYNCHUS KISUTCH DIETS IN CREEK AND ADJACENT POND POPULATIONS. **Noboru Minakawa** and **Gerald Kraft**, Western Washington University. **(30)**

9:30 COMPARISON OF FOOD HABITS OF WILD AND HATCHERY ONCORHYNCHUS MYKISS IN THE YAKIMA RIVER BASIN. **Scott Urakawa, Stamford Smith** and **Paul James**, Central Washington University. **(31)**

9:50 SIMULATING MONOGENIC INHERITANCE IN DROSOPHILA WITH HYPERCARD. **Thomas H. Thelen**, Central Washington University. **(32)**

10:10 - 10:30 Coffee break

10:30 MORPHOLOGICAL DIFFERENCES OF FERRUGINOUS HAWKS IN ALBERTA AND IDAHO. **Daniel N. Gossett** and **M. J. Bechard**, Raptor Research Center, Boise State University. **(33)**

10:50 AGE DETERMINATION AND AGE AT COMPLETION OF METAMORPHOSIS OF THE TAILED FROG, ASCAPHUS TRUEI, **Lucie A. Gray**, Central Washington University. **(34)**

11:10 RED FOX USE OF THE INTERTIDAL ZONE. **Ronald E. Holmes**, Western Washington University. **(35)**

11:30 NODULE AND MYCORRHIZAE FORMATION IN ALNUS RUBRA BY IRRIGATION WITH A STREAM WATER IN THE FOREST. **C.Y. Li** and **Iwan Ho**. USDA Forest Sciences Lab. Corvallis, OR. **(36)**

FORESTRY

Session 1. Thursday morning, 26 March, Bond Hall 112
Presiding: **Brady Green**, U. S. Forest Service

8:30 DORMANCY, COLD HARDINESS, AND STRESS RESISTANCE IN LODGEPOLE PINE (PINUS CONTORTA DOUGL.) SEEDLINGS. **Denis P. Lavender** and **Salim N. Silim**, University of British Columbia. **(37)**

8:50 DORMANCY, COLD HARDINESS, AND STRESS RESISTANCE IN WHITE SPRUCE (PICEA GLAUCA (MOENCH) LAMB.) SEEDLINGS. **Denis P. Lavender** and **Salim N. Silim**, University of British Columbia. **(38)**

9:10 GENETIC VARIATION OF FROST HARDINESS IN WESTERN RED CEDAR (THUJA PLICATA DONN) SEEDLINGS. **Marilyn Cherry**, University of British Columbia. **(39)**

9:30 GENETIC EFFECTS ON WOOD SHRINKAGE IN DOUGLAS FIR (PSEUDOTSUGA MENZIESII (MIRB.) FRANCO). **Matthew P. Koshy** and **Donald T. Lester**, University of British Columbia. **(40)**

9:50 GROWTH RESPONSE SPECIFICITY OF SPRUCE INOCULATED WITH RHIZOSPHERE BACTERIA. **C. P. Chanway** and **B. A. O'Neill**, Forest Sciences, University of British Columbia. **(41)**

10:10 - 10:40 Coffee break

10:40 EFFECT OF SALAL REMOVAL ON TREE HEIGHT GROWTH AND FOLIAGE N: A PRELIMINARY STUDY. **C. M. Preston**, Pacific Forestry Center, Victoria; and **X. C. Chang** and **G. F. Weetman**, University of British Columbia. **(42)**

11:00 RAPID REPEATABLE DETERMINATION OF SOIL MOISTURE IN FOREST CANOPY GAPS USING TIME DOMAIN REFLECTOMETRY (TDR). **Andrew N. Gray**, Oregon State University. **(43)**

11:20 INFLUENCE OF RIPARIAN VEGETATION ON MICROBIAL DEGRADATION OF HERBICIDES IN SOIL. **J. A. Entry** and **W. H. Emmingham**, Forest Science Dept. Oregon State University. **(44)**

11:40 OZONE IN WESTERN WASHINGTON FORESTS. **Felix A. Basabe**, Huxley College, Western Washington University. **(45)**

12:00 noon - 1:30 Luncheon, Viking Union Commons

Session 2. Thursday afternoon, 26 March, Bond Hall 112
Presiding: **Brady Green**, U. S. Forest Service

1:30 CLOUDWATER CHEMISTRY AT STAMPEDE PASS AND THE ALPINE LAKES WILDERNESS AREA. **Linda Cuykendall** and **Felix A. Basabe**, Huxley College, Western Washington University. **(46)**

1:50 WINDFALLS IN THE SIOUXON DRAINAGE, SOUTHWESTERN WASHINGTON. **Charlotte Pyle**, University of Washington. **(47)**

2:10 ECOZONES OF THE NORTHWESTERN CASCADES. **Jan A. Henderson, Robin D. Lesher,** and **David H. Peter**, Mt. Baker-Snoqualmie and Olympic National Forest. **(48)**

2:30 PREDICTING THE LOCATION OF RECREATIONAL-CAUSED FIRES IN SLAVE LAKE PROVINCIAL FOREST, ALBERTA. **Cristina Vega Garcia** and **P. M. Woodard**, University of Alberta; and **B. S. Lee**, NoFC Forestry Canada, Edmonton. **(49)**

2:50 - 3:10 Coffee break

3:10 ENHANCING VEGETATION AND STRUCTURAL DIVERSITY BY MANIPULATING FOREST STANDS. **Ted B. Thomas** and **Andrew B. Carey**, USDA, Pacific Northwest Research Station, Olympia, WA.

3:30 PRIMARY CAVITY EXCAVATORS IN MANAGED ABIES GRANDIS FOREST HABITATS IN WASHINGTON'S EAST CASCADES. **Kenneth R. Bevis**, Central Washington University. **(51)**

3:50 BARKING DAMAGE OF LODGEPOLE PINE. **K. Anre Friedmann**, University of Alberta. **(52)**

4:10 WINTER FOOD CACHING BY MOUNTAIN BEAVERS (APLODONTIA RUFA) IN A GIRDLED DOUGLAS FIR STAND. **J. P. Farley** and **D. L. Campbell**, USDA Animal and Plant Health Inspection Service, Olympia. **(53)**

4:30 EFFECTS OF GRAZING ON HIGH ELEVATION SENSITIVE PLANT HABITATS IN THE OKANOGAN NATIONAL FOREST. **Felix A. Basabe**, Huxley College, Western Washington University. **(54)**

BOTANY

Session 1. Thursday morning, March 26, Bond Hall 106
Presiding: **Rich Fonda**, Western Washington University

8:20 SETTING PLANT COMMUNITY PRESERVATION PRIORITIES: RESULTS OF A 16-YEAR CONSERVATION EFFORT IN WASHINGTON. **Rex C. Crawford** and **Susan Trinh**, Washington Natural Heritage Program, DNR, Olympia. **(55)**

8:40 TAXONOMY AND CONSERVATION OF THE GRAPE FERNS AND MOONWORTS (GENUS BOTRYCHIUM) IN THE PACIFIC NW. **David H. Wagner**, University of Oregon. **(56)**

9:00 STATUS OF RARE PLANT INVENTORY AND PROTECTION EFFORTS IN WASHINGTON STATE. **John G. Gamon**, Washington Natural Heritage Program, DNR, Olympia. **(57)**

9:20 ENDANGERED, THREATENED AND SENSITIVE PLANTS OF FORT LEWIS MILITARY RESERVATION. **Ted B. Thomas** and **Andrew B. Carey**, USDA, PNW Research Station, Olympia. **(50)**

9:40 VEGETATION OF THE NOISY CREED WATERSHED. **Richy J. Harrod** and **Ronald J. Taylor**, Western Washington University. **(58)**

10:00 - 10:20 Coffee break

10:20 RARE PLANTS OF THE WENATCHEE NOUNTAINS, WASHINGTON. **Richy J. Harrod**, USDA, Forest Service, Leavenworth, WA. **(59)**

10:40 RE-CLASSIFICATION OF FOREST AND HIGH ELEVATION RANGE HABITATS IN THE EASTERN NORTH CASCADES OF WASHINGTON. **Therese Bielak** and **Felix A. Basabe**, Western Washington University. **(60)**

11:00 PLANT SURVIVAL BENEATH 1980 TEPHRA FROM MOUNT ST. HELENS. **D. B. Zobel** and **J. A. Antos**, University of Victoria. **(61)**

11:20 INVASION OF INDIGOBUSH (AMMORPHA FRUTICOSA L.) ALONG THE COLUMBIA AND SNAKE RIVERS, WASHINGTON AND OREGON. **Richard R. Halse**, Oregon State University, and **Judith B. Glad**, Portland OR. **(62)**

11:40 STUDYING THE EFFECTS OF MUSHROOM HARVESTING ON CHANTERELLE PRODUCTIVITY IN OREGON'S MT. HOOD NATIONAL FOREST. **Lorelei L. Norvell**, University of Washington. **(63)**

Session 2. Friday morning, March 27, Bond Hall 106
Presiding: **Rich Fonda**, Western Washington University

8:30 VARIATION AND RELATIONSHIPS OF PLANT COMMUNITIES IN THE NORTH CASCADES. **George Wooten** and **Peter Morrison**, USDA, Forest Service, Winthrop WA. **(64)**

8:50 CLIMATE CHANGE AND SUBALPINE TREE GROWTH. **David W, Peterson** and **David L. Peterson**, National Park Service, CPSU, University of Washington. **(65)**

9:10 EFFECTS OF CLIMATE AND OTHER ENVIRONMENTAL FACTORS ON TREE ESTABLISHMENT IN SUBALPINE MEADOWS. **Regina M. Rochefort** and **David L. Peterson**, National Park Service, CPSU, University of Washington. **(66)**

9:30 EFFECTS OF CLIMATE ON REGENERATION OF SUBALPINE FORESTS FOLLOWING WILDFIRE. **Ronda L. Little** and **David L. Peterson**, National Park Service, CPSU, University of Washington. **(67)**

9:50 UNGULATE/FOREST RELATIONSHIPS IN OLYMPIC NATIONAL PARK: RETROSPECTIVE EXCLOSURE STUDIES. **Andrea Woodward, Douglas B. Houston, Edward G. Schreiner,** and **Bruce B. Moorhead**, Olympic National Park. **(68)**

10:10 - 10:40 Coffee break

10:40 EFFECTS OF MINERAL DEFICIENCIES ON PHOTOSYNTHESIS OF SITKA SPRUCE SEEDLINGS. **R. H. Wagner**, University of Washington. **(69)**

11:00 IN VITRO PROPAGATION, CALLUS INDUCTION, AND PROTOPLAST ISOLATION OF MELALEUCA ALTERNIFOLIA. **Tze-Huey Wah** and **Hubertus Kohn**, Western Washington University. **(70)**

11:20 PLANT SPACE BEHAVIOR CONFIRMS W-WAVE HYPOTHESIS. **O. E. Wagner**, Wagner Research Lab., Rogue River, OR. **(71)**

11:40 OTHER HARMONICS IN PLANT SPACING. **O. E. Wagner**, Wagner Research Lab., Rogue River, OR. **(72)**

VERTEBRATE BIOLOGY

Session 1: Taxonomy, Distribution, and status of Terrestrial Vertebrates in the Pacific Northwest. Thursday afternoon, 26 March, Bond Hall 106

Presiding: **John J. Lehmkuhl**, USDA, Forest Service

1:30 THE DISTRIBUTION AND STATUS OF POND TURTLES IN WESTERN WASHINGTON. **Harriet Allen**, Washington Department of Wildlife, Olympia. **(73)**

1:50 THE PAST DISTRIBUTION AND CURRENT STATUS OF THE SPOTTED FROG (RANA PRETIOSA) IN WESTERN WASHINGTON. **William P. Leonard**, Washington Department of Ecology. **(74)**

2:10 DISTRIBUTION AND STATUS OF THE FISHER IN WASHINGTON. **Keith B. Aubry**, USDA, Forest Service, Olympia, and **Douglas B. Houston**, National Park Service, Olympic National Park. **(75)**

2:30 DISTRIBUTION OF PYGMY RABBIT (BRACHYLAGUS IDAHOENSIS) BURROWS IN SAGEBRUSH FLATS, WASHINGTON. **Megan L. Gahr**, University of Washington. **(76)**

2:50 DISTRIBUTION AND SPECIATION PROBLEMS WITH POCKET GOPHERS (THOMOMYS SPP.) IN OREGON AND WASHINGTON. **Gary Witmer**, USDA Animal and Plant Health Inspection Service, Olympia. **(77)**

3:10 - 3:30 Coffee break

3:30 DISTRIBUTION AND STATUS OF SEALS IN PUGET SOUND. **Stephen Jeffries**, Washington State Department of Wildlife, Tacoma. **(78)**

3:50 WASHINGTON STATE SHRUB STEPPE ECOSYSTEM STUDIES;WITH EMPHASIS ON AVIAN SPECIES OCCURRENCE, DENSITIES AND DIVERSITY. **Frederick C. Dobler**, Washington State Department of Wildlife. **(79)**

4:10 STATUS AND DISTRIBUTION OF BALD EAGLES IN WASHINGTON. **James W. Watson**, Washington Department of Wildlife, Mill Creek. **(80)**

4:30 STATUS OF GREAT BLUE HERON NESTING COLONIES IN KING COUNTY WASHINGTON. **Henning Stabins** and **Kenneth Raedeke**, Raedeke Associates Inc., Seattle. **(81)**

4:50 SPECIES COMPOSITION OF TWO OREGON CENTRAL COAST GULL (LARUS SP.) FLOCKS. **Kathy Merrifield**, Oregon State University. **(82)**

Session 2: General Vertebrate Biology. Friday morning, 27 March, Bond 112
Presiding: **John F. Lehmkuhl**, USDA, Forest Service

8:00 PRELIMINARY OBSERVATIONS OF NESTING RAVENS (CORVUS CORAX) ON SAN JUAN ISLAND, WASHINGTON. **Linda T. Campbell**, Friday Harbor, WA. **(83)**

8:20 STUDIES OF THREE TRANSLOCATED POPULATIONS OF THE WESTERN FENCE LIZARD IN NORTHERN PUGET SOUND. **H. A. Brown**, Western Washington University. **(84)**

8:40 SENSITIVITY OF POPULATION GROWTH RATES TO LIFE HISTORY COMPONENTS FOR MEDIUM-SIZED MAMMALS. **James B. Hallett**, Washington State University, and **Margaret A. O'Connell**, Eastern Washington University. **(85)**

9:00 EDGE EFFECTS ON SMALL MAMMALS IN FOREST REMNANTS OF SW OREGON. **L. Scott Mills**, University of Calif., Santa Cruz. **(86)**

9:20 LOG USE BY CALIFORNIA RED-BACKED VOLES. **David A. Tallmon** and **L. Scott Mills**, University of Calif., Santa Cruz. **(87)**

9:40 HYPOGEOUS SPOROCARPS IN MANAGED AND UNMANAGED FORESTS OF SOUTHWESTERN OREGON: COARSE WOODY DEBRIS-FUNGAL-SMALL MAMMAL INTERRELATIONSHIPS. **David A. Clarkson**, Marlboro College, Vermont; and **L. Scott Mills, Michael P. Amaranthus,** and **Jennifer Ramstetter**, University of Calif., Santa Cruz. **(88)**

10:00 - 10:20 Coffee break

10:20 ABUNDANCES OF SMALL MAMMALS IN OLD AND YOUNG FORESTS ON THE OLYMPIC PENINSULA. **Andrew B. Carey**, Pacific Research Station, Olympia. **(89)**

10:40 EXPERIMENTAL MANIPULATION OF MANAGED STANDS TO PROVIDE HABITAT FOR SPOTTED OWL AND TO ENHANCE PLANT AND ANIMAL DIVERSITY. **William L. Kerschke** and **Andy B. Carey**, USDA, PNW Research Sta. Olympia. **(90)**

11:00 ECOLOGY OF THE WESTERN GRAY SQUIRREL (SCIURIUS GRISEUS) ON FORT LEWIS MILITARY BASE. **Lori A. Ryan** and **Andrew B. Carey**, USDA, PNW Research Station, Olympia. **(91)**

11:20 NEST SITES OF NORTHERN FLYING SQUIRRELS IN MANAGED SECOND-GROWTH FORESTS. **Todd M. Wilson** and **Andrew B. Carey**, USDA, PNW Research Station, Olympia. **(92)**

11:40 USING BIOTELEMETRY TO MEASURE MORTALITY SOURCES IN ELK. **Jack L. Smith, Warren A. Michaelis, and Kreg Sloan**, Washington Dept. of Wildlife, Olympia. **(93)**

LICHENS AND MOSSES

Session 1. Thursday afternoon, 26 March, Bond Hall 103
Presiding: **Fred Rhoades**, Western Washington University

2:20 GLOBAL PERSPECTIVE ON ENDANGERED BRYOPHYTES. **John A. Christy**, Oregon Natural Heritage Program, Portland. **(94)**

2:40 DISTRIBUTION OF SOME COMMON FOREST LICHENS ON THE OLYMPIC NATIONAL FOREST. **Robin D. Lesher** and **Jan A. Henderson**, Mt. Baker-Snoqualmie and Olympic National Forest, USDA, Forest Service. **(95)**

3:00 USE OF LICHENS BY WILDLIFE IN NORTH AMERICA. **Stephen Sharnoff**, Missouri Botanical Garden. **(96)**

3:20 - 3:40 Coffee break

3:40 LICHEN REGENERATION FOLLOWING LOGGING IN CARIBOU WINTER HABITAT IN WEST CENTRAL ALBERTA. **J. M. Snyder** and **P. M. Woodard**, Univ. of Alberta. **(97)**

4:00 ECOLOGY AND SUCCESSIONAL STATUS OF TERRESTRIAL AND ARBOREAL LICHENS ON THE WINTER RANGE OF THE ITCHA/ILGACHUZ CARIBOU. **A. R. Brulisauer** and **M. D. Pitt**, University of British Columbia. **(98)**

4:20 LICHENS OF THE FREMONT NATIONAL FOREST, SOUTH-CENTRAL OREGON. **Bruce Ryan**, Smithsonian Institute. **(99)**

4:40 A GUIDE TO NORTH AMERICAN LICHENS. PREVIEW OF ILLUSTRATIONS FOR THE FORTHCOMING HANDBOOK BY IRWIN BRODO. **Silvia Duran Sharnoff** and **Stephen Sharnoff**, Missouri Botanical Garden.

Session 2. Friday morning, 27 March, Bond Hall 103
Presiding: **Fred Rhoades**, Western Washington University

8:40 CHANGES IN RELATIVE FREQUENCY OF EPIPHYTIC LICHEN SPECIES ON OAK AND ASH TWIGS IN WESTERN OREGON, 1971 TO 1991. **Jan Palmer-Muller, Francisco J. Camacho, Stephen C. Sillett,** and **William C. Denison**, Oregon State University. **(101)**

9:00 DISTRIBUTIONS OF BRYOPHYTES AND LICHENS ON GARRY OAK TRUNKS. **Michael W. Ryan**, University of Victoria. **(102)**

9:20 NEW TRANSPLANT METHODS FOR EPIPHYTIC LICHENS. **Chiska C. Derr** and **Bruce McCune**, Oregon State University. **(103)**

9:40 BIODIVERSITY OF THE SPECIES USNEA LONGISSIMA; TESTING FOR CHEMOTYPES AND DYE CHARACTERISTICS. **Sherman G. Brough**, University of British Columbia. **(104)**

10:00 - 10:20 Coffee break

10:20 LIST OF NAMES IN CURRENT USE (NCU) IN CLADONIACEAE: A PROJECT TO AID IN STABILIZATION OF NOMENCLATURE. **Teuvo T. Ahti**, Univ. of Helsinki, Finland. **(105)**

10:40 MULTIVARIATE ANALYSES OF ELEMENTAL CONTENT IN LICHENS OF OLYMPIC NATIONAL PARK, WASHINGTON. **Fred Rhoades**, Western Washington University. **(106)**

11:00 A FLORISTIC SURVEY OF THE EPIPHYTE COMMUNITIES INHABITING THE CROWNS OF TWO OLD-GROWTH CONIFERS IN REDWOOD NATIONAL PARK, CALIFORNIA. **Stephen C. Sillett**, Oregon State University, and **T. Scott Sillett**, Louisiana State University. **(107)**

11:20 VERTICAL SUCCESSION OF EPIPHYTES IN DOUGLAS FIR - HEMLOCK FORESTS. **Bruce McCune**, Oregon State University. **(108)**

11:40 PRELIMINARY OBSERVATIONS ON "ANTIQUE" FORESTS AND EPIPHYTIC MACROLICHEN DIVERSITY IN BRITISH COLUMBIA. **Trevor Goward**, University of British Columbia. **(109)**

HYPOGYMNIA WORKSHOP

Friday afternoon, 1:30-5:00, 27 March, Haggard Hall 315

FIELD TRIPS

Saturday, 28 March. All field trips will leave from the Haggard Hall Parking Ramp, on High Street at the time indicated below. Return time is an estimation. Lunches are provided.

Skagit Wetlands/Padilla Bay - Departure time: 9:00 A.M., return time: ca. 3:00 P.M.

Sulfur Creek lava flow - SE side of Mt. Baker, about a 1 1/2 hour bus ride from Bellingham; emphasis on mosses and lichens. Departure time: 9:00 A.M., return time: ca. 4:00 P.M.

Noisy Creek old-growth forest - Above (SE) Baker Lake, about a 1 1/2 hour bus ride from Bellingham to Shannon Creek Camp Ground plus a boat trip across the lake. Departure time: 8:30 A.M. return time: ca. 4:00 P.M.

1

LANDSCAPE MANAGEMENT IN A CHANGING ENVIRONMENT. David L. Peterson, National Park Service Cooperative Park Studies Unit, University of Washington, Seattle.

The preservation of protected areas may become more difficult in the future if there are rapid changes in the atmospheric environment of the earth. Climate change could result in future ecosystems that are quite different than those that exist today. Recent changes in the growth and distribution of subalpine tree species in western North America suggest that some changes may have already occurred. Ecosystem dynamics are complex and rarely in temporal or spatial equilibrium with the physical environment. A management strategy that focuses on landscapes is preferable to one that attempts to protect ecosystems from change. Protecting a diverse landscape with multiple landforms will insure a maximum number of habitats, refugia, and sources for plant and animal species. This strategy can be complemented by mitigation that enhances survival of individual species.

2

BIOLOGICAL DIVERSITY AND FOREST MANAGEMENT: A LOOK TO THE FUTURE. Ross Kiester, USDA Forest Service, PNW, Corvallis.

Biological diversity issues pose enormous challenges to forested land management. Meeting these challenges requires understanding the goals for managing for biological diversity, the scientific and technological basis for the management methods, and the trade-offs of managing for biological diversity in the context of other management goals. Deciding on the goals of management for biological diversity must come first and are to be derived from considerations of the use and appreciation of biological diversity. Use may be seen from a human viewpoint or from the viewpoint of the functioning of an ecosystem. Appreciation is largely an aesthetic issue. Possible goals based on use and appreciation and the scenarios of forest management derived from them give insight into the future of forest management.

3

STATUS AND IMPORTANCE OF STOCKS IN THE PACIFIC SALMON RESOURCE. Jim Lichatowich, Consultant, Sequim, WA.

Species of Pacific salmon are comprised of locally adapted stocks. The American Fisheries Society has identified at least 106 stocks that have become exinct. In addition, 101 stocks are at high risk and 58 stocks are at moderate risk of extinction. Another 54 stocks are of special concern. Habitat damage is the most important cause of the decline.

4

ECONOMICS OF BIODIVERSITY: MARKET VALUES

James W. Vincent

University of St. Thomas, St. Paul, MN

There is wide concern that plant and animal diversity is threatened by overexploitation and by destruction of habitat. Of the many concerns relating to this loss is the prospect that the economic value of our biological "capital" is eroding at an excessive rate. The economic value of species diversity manifests itself in many ways. Fisheries, for example, depend on the maintenance of economically viable populations of aquatic species. Recreational value derives from the demand for hunting, fishing, wildlife-watching and a host of other activities. Genetic resources are used for medical purposes, to develop new strains of crops, and for genetic engineering. The question thus arises regarding the aspects of existing economic institutions which promote inefficiently rapid dissipation of biodiversity. The pervasive absence of well-defined and enforceable property rights for naturally occurring biological resources precludes the use of economic incentives to conserve these assets. It is argued that the assignment of a more complete structure of property rights for biological resources would promote the functioning of markets which owe their existence to biological diversity. By permitting the capture of the economic benefits of biodiversity, economic incentives are employed in the protection of this diversity. Although there are many cases for which an economically viable set of property rights is not feasible, such measures can, along with a broad range of other policies, provide a mechanism for the conservation of biological diversity.

5

THE ECONOMICS OF BIODIVERSITY: NON-MARKET VALUES. Daniel A. Hagen, Western Washington University.

Biological diversity yields economic value in a variety of ways. These include use value, option value, quasi-option value and existence value. Some of the economic goods associated with biodiversity are characterized by non-rival consumption, which precludes their efficient allocation in private markets. In addition, such goods are frequently characterized by non-excludability, which inhibits the development of private markets. Under these circumstances, optimal allocation of the good requires collective or public action. A framework is presented for analyzing the level and distribution of the net benefits of preservation through habitat conservation and other measures. The economic benefits of biodiversity accrue internationally, and thus optimal collective action necessarily involves international economic cooperation. Issues examined include the measurement of benefits and costs, alternative international payment mechanisms, and the free rider problem.

6

Edward G. Schreiner 206-452-4501
Research Biologist
Olympic National Park

Biodiversity: A National Park Service Perspective from Olympic National Park

Olympic National Park is an isolated area at the center of the Olympic Peninsula. Steep elevation and precipitation gradients and a maritime climate have lead to development of a fascinating biota. From the National Park Service perspective, biodiversity needs to be evaluated at several levels. The biodiversity of Olympic National Park at the genetic, species and community levels will be discussed in the context of natural area national parks. A classification scheme for regionally rare plants will be presented.

7

WASHINGTON DEPARTMENT OF NATURAL RESOURCES' STRATEGY FOR THE PROTECTION OF BIODIVERSITY. Mark Sheehan WDNR Natural Heritage Program, Olympia.

The WDNR has several programs for the protection of biodiversity. The Natural Heritage Program maintains a comprehensive data base of high quality and rare elements of natural diversity, including plant species, plant communities and wetlands. These data are used in protection activities, such as land acquisition and voluntary protection. The Natural Area Preserves (NAPs) and Natural Resources Conservation Area (NRCAs) are areas set aside for the protection of biodiversity. NAPs are established to protect undisturbed terrestrial and aquatic ecosystems, rare species and unique geological features; for research and education; as gene pools reserves; and to serve as baselines to compare to more managed systems. NRCAs, while established primarily to protect ecological features, allow more low impact public use. New protection policies for state-owned forest lands are being reviewed for addition to the Forest Resource Plan.

8

CONSERVING BIODIVERSITY AT THE LANDSCAPE LEVEL: CHOICES IN THE MANAGED FOREST. Peter T. Haug, Washington Department of Wildlife.

The Forest Practices Board and participants in the Timber/Fish/Wildlife Agreement have been working cooperatively to assess cumulative effects of forest practices on public resources in Washington. Part of this effort has focused on developing a method to analyze the landscape mosiac across a watershed for possible effects on wildlife. Known wildlife/habitat relationships are used to identify vegetative types and seral stages that provide essential habitat for wildlife species most at risk. Landscape parameters such as patch size, shape, contrast, juxtaposition, interspersion, and connectedness through corridors are used to characterize watersheds with respect to wildlife habitat. Innovative silvicultural techniques are recommended for modifying structural characteristics of patches to emulate different successional stages and improve biodiversity within a watershed. The method shows promise for creating a moving "template" in a basin to accommodate wildlife needs by recognizing dynamic characteristics of a managed forest resulting from harvest, reforestation, and natural succession.

9

MARS AFTER VIKING: POSSIBILITIES FOR LIFE. David J. Thomas, Central Washington University, and Joshua P. Schimel, Institute of Arctic Biology.

The results of the Viking biology and organic chemistry experiments seemed to rule out the possibility of life on Mars. We present a hypothetical model of Martian ecology based on the premises that Martian life could be endolithic, and that it could undergo long periods of dormancy. We also review new evidence which supports the possibility of life in hostile environments similar to that of Mars.

10

THE DISPOSAL OF HOUSEHOLD HAZARDOUS WASTE: RESULTS FROM A SURVEY OF PIERCE COUNTY, WASHINGTON

David A. Swanson, Center for Social Research, Pacific Lutheran University, Tacoma, WA

This study examines disposal practices involving five types of household hazardous waste using data from a 1989 survey of 804 randomly selected households in Pierce county, Washington. The association between unsafe disposal practices and each of three sociodemographic variables is also examined. The findings indicate that many households usually use unsafe disposal methods for the three hazardous wastes covered in the survey that are directly related to households: cleaning agents; paints/solvents; and pesticides/herbicides. Far fewer use unsafe disposal practices for the two types of hazardous waste directly related to personal transportation: antifreeze; and used automobile oil. An inverse relationship is found between age and unsafe disposal practices but no relationship is found between gender and unsafe disposal practices. The third sociodemographic variable is a proxy for the level of social integration a person has with his or her community. An inverse relationship, which was hypothesized for the level of social integration and unsafe disposal practices, is found to exist between the proxy variable (Whether or not a person plans to be in the same community in five years) and unsafe disposal of each of the five types of household hazardous waste. It is argued that similar findings are likely to be found in metropolitan areas throughout the U.S. Further, the findings lend support to Cassel's observation that state governments must face the need to find alternatives to cost-ineffective Household Hazardous Waste disposal programs in spite of their perceived public support.

11

Alkali Lake, OR: Geology of a Toxic Waste Site. Kenneth A. Cameron, Geologist, Oregon Department of Environmental Quality

Between 1969 and 1971 25,000 barrels of herbicide waste were stored on the edge of Alkali Lake playa in south-central Oregon. In 1976 the State of Oregon ordered the barrels pushed into trenches, crushed, and covered. The rational was that this was a closed basin in a semi-desert environment and contaminants would not travel far. In actuality, the basin is part of Basin and Range physiography and is cut by numerous faults traceable on infrared photographs by vegetation variations. An artesian aquifer which feeds springs along the fault traces forms in Pliocene volcanics underlying lacustrine sediments of the playa. Hutton Spring, 3 miles north of the site, is inhabited by the endangered Tui chub. Strong groundwater flow driven by fault directed artesian water is pushing the contamination in the opposite direction than anticipated and the plume has now reached and come to the surface at West Alkali Lake, a distance of ½ mile.

12

PRELIMINARY INVESTIGATION OF GARDNER CAVE, PEND OREILLE COUNTY, WASHINGTON. Eugene P. Kiver, John P. Buchanan, Brenda R. Gibson, William A. Graham, Iain A. Olness, and Richard Severn Eastern Washington University.

A university class surveyed and studied a recently discovered extension of Gardner Cave. The cave system has 490 m of passage and follows the 21° SW dip of the Middle Cambrian Metalline Limestone. Evidence suggests that a coarse fill of outwash(?) gravel was followed by speleothem formation, partial removal of fill, and a later fill by fine-grained sediment. A ceiling channel was cut atop the sediment fill and the present episode of speleothem deposition followed partial removal of fill material. Coarse and fine fills may have occurred more than once. Radiometric dates (Martin 1989) are compatible with cave formation during the last interglacial and Holocene deposition and removal of the fine cave fill. More detailed study of the cave sediment and geomorphic features will improve our understanding of the influence of Pleistocene glaciers, topographic factors, and groundwater hydrology on speleogenesis.

13

The November 1990 Flood in South Western British Columbia, An Overview of the Restoration Process

C. Robert Bland, P. Eng.

The November 1990 flood caused widespread damage to rivers in southwestern British Columbia. Restoration works were assessed on a site by site basis by a team of engineers and environmentalists.

While a "people versus fish" conflict was evident, the team approach ensured that the restoration work was carried out with minimal environmental damage.

14

Hydrologic Simulation of the Lake Whatcom watershed. Steven J. Walker, Institute for Watershed Studies, Huxley College, Western Washington University, Bellingham Washington.

The Hydrologic Simulation Program - FORTRAN (HSPF) was adapted for use in the Lake Whatcom watershed. The watershed was divided into hydrologically homogenous land areas based upon watershed soils and land use/cover data layers. Utilizing the ODYSSEY geographic information system, land surface attributes were overlain and contributing areas ascertained. The set of HSPF model parameters were estimated based upon the matrix of watershed physical conditions and sub-basin boundaries. The model was driven by continuous daily precipitation and potential evapotranspiration time series. Model output was calibrated to two years of continuous historical streamflow data for three creeks within the watershed. The calibrated model was utilized for prediction of the 1990-1991 water budget for the watershed.

15

EFFECTS OF CYST DENSITY AND AGE ON THE SEDIMENTATION OF GIARDIA CYSTS. Enikö A. Kramár, Central Washington University

Currently, to recovery *Giardia* cysts from water a reference procedure is used which requires a centrifugation step of 600 x g for 5 minutes to concentrate the cysts. Findings in our lab indicate that a significant proportion of *Giardia* cysts do not sediment under these conditions and would be discarded using the reference method. The first objective in this present study is to determine the centrifugation conditions needed to pellet the majority of *Giardia* cysts in an aqueous solution. Sedimentation of *Giardia* cysts at different centrifuged forces and at different centrifugation times is being investigated. The number of *Giardia* cysts in both the sediment and supernatant fractions is determined using a membrane filtration staining procedure. Results obtained indicate that centrifugal forces and/or centrifugation times greater than those used in the reference method are needed to sediment all of the *Giardia* cysts from an aqueous suspension. The effects of cyst density and cyst age on sedimentation are being investigated. A second objective of this study is to determine the density of *Giardia lamblia* cysts using a Percoll gradient and density marker beads. These studies are in progress.

16

ENVIRONMENTAL CUES AND THE REPRODUCTIVE CYCLES OF THREE TEMPERATE ASCIDIAN SPECIES. Brian L. Bingham Shannon Point Marine Center, Anacortes, WA.

The reproductive cycles of three ascidian species (Boltenia villosa, Chelyosoma productum, and Styela gibsii) were studied for 12 months to determine what environmental factors are responsible for long-term reproductive synchrony. Neither seawater properties (i.e. temperature, salinity) nor phytoplankton abundance were strongly correlated with gonad growth or maturation. However, the observed patterns of gonad maturation were related to photoperiod and day length. We manipulated light cycles in the laboratory and compared gonad indices (% wet body weight) and oogenesis in animals exposed to a natural light cycle and those in a reversed light treatment. Significant differences were found between the two groups with the gametogenic cycles of the reversed-light animals being thrown out of phase in seasonally spawning species. These results indicate that day length, in addition to serving as a proximal spawning cue in some ascidians, may also play an important role in longer-term reproductive synchronization.

17

THE DEVELOPMENTAL AND PHYSIOLOGICAL RESPONSE OF CANCER MAGISTER MEGALOPAE TO DIEL CYCLES OF TEMPERATURE AND SALINITY. MATTHEW W. JOHNSON. WESTERN WASHINGTON UNIVERSITY.

In Washington, the Dungeness crab, Cancer magister is separated into at least two populations, those found on the outer coast and those in the waters of the Puget Sound basin, including Georgia Strait. Previous studies have identified distinct developmental differences in the megalopae. Because of the potential for gene flow between the two areas, larval differences are likely to be phenotypic. The amount of mixing and freshwater runoff in the two areas results in very different surface salinities and temperatures. Because of the vertical migration, the megalopae in the two areas will experience different temperature and salinity cycles. The experiment exposed the megalopal larvae to three diel cycles of salinity and temperature to determine its effects on time to molting, survival, growth, and respiration. Initial analysis suggests that the cycles do effect respiration and time to molting. Trends indicate a delay in the time until molting of the 9-18C temperature cycle as compared to both the 9-18C cycle with a salinity cycle and the 10-13C temperature cycle.

18

NUTRITIONAL ANALYSIS AND EFFECT OF CRUDE OIL ON THE LARVAL DEVELOPMENT OF HEMIGRAPSUS OREGONENSIS. Mary Jo Hartman Western Washington University.

Hemigrapsus oregonensis is a brachyuran shore crab whose habitat extends from Alaska to California. This study examined the nutritional requirements and the effect of oil pollution on the development of the zoeae. Individual larvae were raised in the laboratory on one of three diets; the rotifer Brachionus plicatilis, cultured on the green alga Dunaliella tertiolecta; Brachionus plicatilis, cultured on the golden brown alga Isochrysis galbana; and freshly-hatched nauplii of the brine shrimp Artemia sp. Starvation resistance of larvae was also examined. Preliminary results show no differences in the zoeae due to oil contamination of the pre-ovigerous females. Larvae raised on the Isochrysis galbana-fed rotifers appear to have the highest survival rates, highest megalopae dry weights and lowest mean day to molt. Molt frequency was affected by the starvation regime.

19

GROWTH OF THE RED TIDE ALGA HETEROSIGMA AKASHIWO. Chris N. Fairbanks Western Washington University.

Blooms of this single celled alga have recently caused severe loss of fish in net pen fish farms. Blooms result from rapid growth of phytoplankton under ideal conditions of nutrients, temperature, and light. Growth requirements of this alga are not well understood. This work investigates the effect of temperature and light on the growth rate of laboratory cultures of H. akashiwo. Growth was measured over five temperatures (10-20°C) and four light intensities (0.8 - 235.5 μE). Preliminary results suggest that growth rate is dependent on temperature, increasing with temperature. Doubling time was 6.2 days at 10°C, and 0.7 days at 20°C. Light intensity is less important. These results suggest that the growth of H. akashiwo in the inland waters of Washington State is limited primarily by temperature and somewhat by light intensity.

20

CLAM SPECIES AND VERTICAL DISTRIBUTION ON A COARSE AND FINE SEDIMENT BEACH IN PUGET SOUND WASHINGTON. DOUGLAS P. HANSON CENTRAL WASHINGTON UNIVERSITY

A transect study of clam species distribution and substrate composition was undertaken on two beaches in the Puget Sound region. Clam species were classified according to the type of substrate they inhabited and their position on the beach. General correlations were observed between clam species and sediment size. The study investigated possible reasons each specie preferred a type of substrate for a habitat. Application of this study could lead to the development of guidelines for providing suitable habitat for each clam specie.

21

THE SPAWNING DYNAMICS OF WALLEYE POLLOCK, THERAGRA CHALCOGRAMMA, IN SHELIKOF STRAIT, GULF OF ALASKA

Nazila Merati
NOAA-Fisheries
Seattle, Washington

The spawning dynamics of female walleye pollock, Theragra chalcogramma, in the Shelikof Strait, Gulf of Alaska were studied in 1990. The purpose of this study was threefold; first, to characterize spawning dynamics of this fishery. Secondly, to determine the age at first maturity in female fish. Lastly, to develop a immunochemical assay to assess reproductive condition and to test this assay against other more established methods to determine sexual maturity stage. At this time, an antibody to egg-yolk protein has been developed, native egg proteins have been characterized and an assay has been developed. The assay may be useful in distinguishing between immature and spent/recovering maturity stage. These stages are difficult to determine by visual inspection.

22

RNA/DNA RATIOS AS INDICATORS OF NUTRITIONAL CONDITION OF LARVAL WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*.

MICHAEL F. CANINO AND KEVIN M. BAILEY, Alaska Fisheries Science Center, NOAA, Seattle.

Food consumption and nucleic acid ratios of first-feeding pollock larvae in the Gulf of Alaska were sampled during early spring and mid-spring, 1989. A large patch of larvae was detected. Mean prey abundance, gut contents (prey larva^{-1}) and RNA/DNA values of larvae were higher within the patch than in areas outside the patch during early spring. By mid-spring, microzooplankton densities, feeding intensity and RNA/DNA of larvae both inside and outside of the patch had increased. The results indicate a linkage between food availability, feeding, and growth during early periods of larval development.

23

MANAGEMENT ADVICE FROM A SIMPLE DYNAMIC POOL MODEL WHEN STOCK-RECRUITMENT PARAMETERS ARE UNCERTAIN.

Grant G. Thompson, National Marine Fisheries Service, Seattle, WA

A simple dynamic pool model is used to examine the problem of stock-recruitment parameter uncertainty from a Bayesian perspective. Probabilities associated with different parameter values are used to weight the losses (i.e., opportunity costs to society) associated with any given fishing mortality rate. By choosing appropriate forms for the loss and probability density functions, the model is shown to result in an analytic solution. Because this solution gives the fishing mortality rate that maximizes the expected value of the logarithm of sustainable yield, it is denoted F_{MELSY}. The solution is a monotone decreasing function of parameter uncertainty, converging on the fishing mortality rate corresponding to maximum sustainable yield as the degree of uncertainty approaches zero. As an empirical illustration, the model is applied to the eastern Bering Sea stock of rock sole (*Lepidopsetta bilineata*).

24

EFFECTS OF UVBR ON SURVIVAL OF MEDAKA EMBRYOS.

Andrea J La Tier and Jack Hardy. Huxley College, Wastern Washington University, Bellingham.

Medaka embryos were exposed to ultraviolet radiation (280-320 nm) UVBR, predicted to result from 13%, 25% and >25% (+/- 5%) reductions in stratospheric ozone (Oe3). Doses approximated those for clear skies at the water surface in July at 40N (Green et al., 1980). UVBR and photosynthetically active radiation (PAR) were generated using UV-B 313 and Gro-Lux bulbs. Exposure was electronically modulated using a sinusoidal dimming ballast linked to a controller designed to simulate a natural diurnal spectral curve. Wavelength-specific irradiances were converted to total dose, weighted by a DNA action spectrum (Setlow, 1974) and normalized to 300 nm (UVBR DNA 300). A dose rate (2,436 J/M2/day) equivalent to a 13% reduction in stratospheric O3 was sufficient to cause complete mortality of medaka embryos after 10 days of exposure.

25

DISTRIBUTION AND SUMMER STANDING CROP OF SEAGRASSES AND MACROALGAE IN PADILLA BAY, WASHINGTON, 1989.

Douglas A. Bulthuis, Padilla Bay National Estuarine Research Reserve, Washington Dept Ecology, Mount Vernon, WA

The channels, seagrass and macroalgal beds and intertidal flats in Padilla Bay, Washington were mapped during summer, 1989. Seagrasses, principally Zostera marina L., covered about 3000 hectares in Padilla Bay. Zostera japonica Aschers. & Graebn. was distributed higher in the intertidal than Z. marina and covered about 300 hectares. The seagrass, Ruppia maritima, reported from Padilla Bay for the first time, is widely distributed at a very sparse density over about 140 hectares. Large accumulations of Ulva and Enteromorpha covered about 220 hectares in the southern part of Padilla Bay. Density of Zostera marina ranged up to 441 shoots m^{-2} and for Z. japonica up to 1095 shoots m^{-2}. Standing crop of seagrasses ranged from 12 to 103 g dry weight m^{-2} at 13 seagrass covered sites at which macroalgae biomass ranged from less than 1 to 190 g dry weight m^{-2}. The seagrass beds in Padilla Bay are one of the largest contiguous beds of seagrass in Washington and along the Pacific Coast of North America.

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HOW DIFFERENT ARE SAND DOLLARS? AN EXAMINATION OF THE ORAL-SURFACE PODIA AND SIEVE HYPOTHESES IN DENDRASTER EXCENTRICUS.

D.C. Williams Western Washington University, Bellingham,

Oral and aboral surface hydrolases (amylase, cellulase and protease) were measured in the sand dollar (Dendraster excentricus), seastar (Pisaster ochraceus) and sea urchin (Strongylocentrotus droebachiensis). Measurement provided no evidence for the uniqueness of the sand dollar oral and aboral surface in contributing to pre-ingestion digestive events of macro- or micronutrients. In addition, relative concentrations of the indicated digestive hydrolases were determined in the small and large intestines of the sand dollar. The small intestine is the site of major digestive hydrolase activity.

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DELAYED HATCHING OF SQUID AS A RESULT OF REDUCED LIGHT LEVEL.

William C. Summers, Western Washington University, Bellingham, WA 98225.

Eggs of the sepiolid squid, Rossia pacifica, were hatched at near-surface, light levels and cycles, and in nearly continuous darkness to simulate shallow and deep conditions. Six clutches of trawled and aquarium laid eggs were divided into each treatment and hatching monitored over one-half year in running seawater. In cultivation, hatching extends no more than 3 months (98%), but it can be twice that long. It is keyed to the lunar cycle, which is maintained in the dark, and is delayed about one month in the dark treatment.

Because this species is known to occur at a wide depth range and lacks a planktonic juvenile stage, hatching of eggs laid far below the photic zone would be out of synchrony with those laid at shallow depths based on light effects alone. At all simulated depths, hatching near the time of the new moon assures minimal opportunity for visual predators and dispersal of newly hatched squid.

This result is of importance when compared with other known cephalopods.

28

PHONOTACTIC RESPONSE IN ORTHOPTERANS: SYLLABLE DISCRIMINATION OF FEMALES IN THE CALLING SONG OF MALE HOUSE CRICKETS - ACHETA DOMESTICUS .

Gary D. Lorenson Central Washington University, Ellensburg.

This study, experimental in design, strives to discover the relationship of number of syllables per chirp of a stridulating male Acheta domesticus to the phonotactic response of a conspecific female. The response of the female to synthetically presented typical and atypical syllable numbers in an otherwise normal calling song were compared to control groups with no sound. The results seem to strengthen previous work done in this field on the typical number of syllables per chirp (3) found in the natural calling song. The data does, however, suggest that this population of house crickets will also respond significantly to atypical numbers of syllables per chirp (5) which has previously not been established. This study investigates this anomaly and recommends future exploration of this parameter to establish a more definitive conclusion.

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AN EVALUATION OF ASSOCIATIONS BETWEEN MACROINVERTEBRTES AND MACROPHYTES IN CANNERY POND. Jenifer K. Parsons Western Washington University.

Samples from six species of emergent, floating leaved, and submerged macrophytes were collected from a shallow freshwater pond during the summer of 1990. All macroinvertebrates collected with the plant material were counted; macroinvertebrate subsamples were dried and weighed. Macroinvertebrate abundances and biomass were greatest on submerged plants and highest in midsummer. Many of the macroinvertebrate taxa such as damselflies, chironomid flies, and various species of snails were common on all plants. However, some macrofauna were associated with specific plants. For example, all lepidopteran larvae were found on *Polygonum hydropiperoides*, and the greatest abundance of crustaceans were collected on *Potomogeton natans*. Macroinvertebrate biomass and abundances were not consistently related to available plant surface area or leaf morphology.

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JUVENILE ONCORHYNCHUS KISUTCH DIETS IN CREEK AND ADJACENT POND POPULATIONS. Noboru Minakawa and Gerald Kraft Western Washington University.

Juvenile coho salmon reside in fresh water for at least one year. The diet of a coho population residing in Baker Creek, WA was compared with the diet of a population in a nearby man-made pond on four different dates in November, 1988 through January, 1989. Both populations ate larger numbers of prey when there was high rainfall prior to the sampling dates in November and December. Terrestrial invertebrates were equally abundant in diets of both populations on three of the four sampling dates. Both populations fed heavily on Collembola during late fall and early winter; taeniopterigids and simuliids (stream) and chironomids (pond) were prevalent in January. Temperature, and rainfall seemed to influence diet.

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COMPARISION OF FOOD HABITS OF WILD AND HATCHERY ONCORHYNCHUS MYKISS IN THE YAKIMA RIVER BASIN. Scott Urakawa, Stamford Smith and Paul James Central Washington Unversity

Proposed supplementation of native anadromous Oncorhynchus mykiss in the Yakima Basin has led to questions regarding the potential competition between hatchery-reared fish and both wild resident O. mykiss and wild anadromous O. mykiss populations. A two year study began in the spring of 1991 in an attempt to answer some of these questions. Samples of wild O. mykiss and hatchery O. mykiss were obtained at four different periods during 1991. Gut contents were analyzed to determine the similarity of diets between wild and hatchery O. mykiss Preliminary results show some subtle, but important differences in diet between the hatchery and the wild fish.

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SIMULATING MONOGENIC INHERITANCE IN DROSOPHILA WITH HYPERCARD. Thomas H. Thelen. Central Washington University, Ellensburg.

Crossing fruit flies and observing the resulting phenotypic ratios is an excellent way for students to learn that Mendelian genetics has a basis in reality. Unfortunately the process of generating several generations of flies is so time consuming that a student can seldom study the inheritance of more than a single trait. HyperCard simulations were developed to reduce the time commitment and thereby provide a way to expose students to a variety of traits. Two such simulations which have been used effectively in biology and genetics courses will be demonstrated. The one simulates matings involving any of 45 strains of flies and includes 4 patterns of inheritance, and the other with the same number of strains includes 16 patterns of inheritance,

33

MORPHOLOGICAL DIFFERENCES OF FERRUGINOUS HAWKS IN ALBERTA AND IDAHO. Daniel N. Gossett and M. J. Bechard Raptor Research Center, Department of Biology, Boise State University, Boise, ID 83725.

Twelve female and eleven male adult Ferruginous Hawks (Buteo regalis) were trapped, measured and banded during the 1991 nesting season in southeast Alberta, southcentral and southwest Idaho during the first year of a morphometric study. These birds were trapped using dho-gaza or modified dho-gaza nets placed near the nest sites with an owl or other lure bird placed near the net. Thirty measurements were taken on captured birds. Differences were analyzed by sex and study area. Mass was greater for both sexes of Alberta birds than for Idaho birds. Except for differences in mass, Alberta females were most similar to southwestern Idaho females for several characters including wing length, grasp and bill chord. Birds in dark plumage phase morphology were found to be increased in southcentral Idaho compared to previous studies, with 16.3 percent of adults, and 23.7 percent of nestlings occurring in melanistic plumage. Results are preliminary due to small sample sizes.

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AGE DETERMINATION AND AGE AT COMPLETION OF METAMORPHOSIS OF THE TAILED FROG, ASCAPHUS TRUEI. LUCIE A. GRAY CENTRAL WASHINGTON UNIVERSITY

Past studies have shown that there is variation in the time of metamorphosis among different populations of Ascaphus truei. Coastal populations complete metamorphosis at 2 years of age, many inland populations take 3 years, and recently a population in the northern Cascades has been shown to take 4 years. This study examines the age class structure of eastern Cascade populations of Ascaphus larvae in central Washington. A size-frequency analysis on 495 larvae, collected over a period of 7 months, suggests that they metamorphose at three years of age. An examination of morphological characteristics is currently in progress to determine if there are any discrete larval characteristics that coincide with the size classes, or if any of these size classes may represent more than one age class.

35

RED FOX USE OF THE INTERTIDAL ZONE. Ronald E. Holmes, Western Washington University, Bellingham, Washington.

The objective of this study is to document red fox (*Vulpes vulpes*) use of the intertidal zone as a foraging area, and show the effects of the tide cycle on the activity pattern of the red fox. Observations were taken during daylight hours when fox activity is normally low. A % sighting time was calculated as a measurement of fox activity. The arcsine transformation of % sighting time was regressed against the habitat variable tide amplitude. Red fox use of the intertidal zone during daylight hours, when the tide level is descending, was positively correlated with tide amplitude, $r^2 = 0.41$, $p = .003$. A comparison(ANOVA) of fox use of the intertidal zone during ascending vs. descending tides showed a significantly higher use during descending tides, 4.1% vs 29.6%, $p = 0.008$. The correlation of % fox sighting time to tide amplitude increased over the summer(May-July)then dropped in August when a non-intertidal forage item (blackberries) became available. In the study area, in early-mid summer, the tide cycle has the effect of increasing red fox use of daylight hours for foraging when tide amplitude is high and tide level descending during daylight hours.

36

NODULE AND MYCORRHIZAE FORMATION IN ALNUS RUBRA BY IRRIGATION WITH A STREAM WATER IN THE FOREST. C. Y. Li and Iwan Ho USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corvallis, Oregon 97331

This study was initiated to determine if Frankia and mycorrhizal inocula can be disseminated by the stream water in the forest. Young seedlings of A. rubra in the greenhouse were irrigated with water collected from a creek in the forest. After three months, entire root systems were examined for nodules and mycorrhizae. Seedlings irrigated with the stream water developed nodules and ecto-mycorrhizae while seedlings irrigated with filtered stream water developed no nodules and mycorrhizae and showed stunted growth. Thus the stream water in the forest is the good source of Frankia and mycorrhizal inocula for A. rubra and contributes to natural regeneration of A. rubra along stream bank and beyond.

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DORMANCY, COLD HARDINESS, AND STRESS RESISTANCE IN LODGEPOLE PINE (*PINUS CONTORTA* DOUGL.) SEEDLINGS. Denis P. Lavender and Salim N. Silim, University of British Columbia, Vancouver.

The above seedling parameters were studied during the winter of 1991-92. Cold hardiness developed more slowly than it did in white spruce and the maximum hardiness attained (-45°C.) was significantly less than that of spruce (> -60°C). Further, unlike spruce seedlings, the pine seedlings commenced dehardening under natural conditions in January. Release of cold hardiness and bud dormancy were both correlated strongly with duration of exposure of seedlings to temperatures of 5°C., but stress resistance, as measured by the plants' ability to initiate and elongate new roots after a crushing stress, was independent of both cold hardiness and bud dormancy. Stress resistance reached a maximum between late November and early February. Root growth of the control seedlings varied during the experiment but was not generally related to the length of exposure of seedlings to 5°C. temperature.

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DORMANCY, COLD HARDINESS, AND STRESS RESISTANCE IN WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) LAMB.) SEEDLINGS. Denis P. Lavender & Salim N. Silim, University of British Columbia, Vancouver.

The above parameters of white spruce were studied during the winters of 1990-91 and 1991-92. Both the release of dormancy and the development of stress resistance were delayed by the very mild temperatures obtaining during the winter of 1991-92, but the development and degree of cold hardiness were not affected. The release of cold hardiness and of bud dormancy are both strongly correlated ($R^2 > .90$) with the number of degree hours at 5°C. to which the seedlings were exposed and both were initiated after an exposure of about six hundred hours. Seedling resistance to a crushing stress, as measured by the plants' ability to initiate and grow new roots after treatment was not related to cold hardiness but appeared to be influenced by exposure to 5°C. temperature. Maximum stress resistance occurred between late November and early February. Although root growth of the control seedlings varied throughout the experimental period, there was no correlation between total root elongation and duration of seedling exposure to 5°C. temperature.

39

GENETIC VARIATION OF FROST HARDINESS IN WESTERN RED CEDAR (*THUJA PLICATA* DONN) SEEDLINGS Marilyn Cherry, University Of British Columbia, Vancouver.

Frost hardiness testing was conducted for two seasons on one-year-old and two-year-old western red cedar (*Thuja plicata* Donn) seedlings which were grown in Vancouver. Eight provenances were sampled with four provenances having family structure (three families per provenance).

Genetic differences occurred on ten test dates per winter between coastal and interior populations, between provenances within populations, and between families within provenances. The rate of hardening and dehardening differed between populations and between provenances.

During the second winter, seedlings became hardy to lower minimum temperatures than in the previous season, but provenance and family rankings were similar for the two years.

40

GENETICS EFFECTS ON WOOD SHRINKAGE IN DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* (MIRB.) FRANCO). Mathew P. Koshy & Donald T. Lester, University of British Columbia, Vancouver.

416 trees belonging to 48 full-sib families were sampled from a 18-yr-old progeny trial (Ministry of Forests, B.C.). Wood shrinkage in three dimensions, longitudinal, transverse and radial, were assessed at different age intervals within the tree, using samples prepared from a bolt taken at breast height of the tree. Shrinkage changed rapidly as a function of age from the pith. Longitudinal shrinkage decreased whereas radial and transverse shrinkage increased. Variation among trees within family was the largest single source of variation. Estimates of proportion of variation that would be transmitted to the progeny (heritability) varied at different age intervals.

41

Growth Response Specificity of Spruce Inoculated with Rhizosphere Bacteria. C.P. Chanway and G.A. O'Neill, Forest Sciences, University of British Columbia.

The influence of rhizosphere bacteria on hybrid spruce (Picea glauca x engelmannii) seedling growth was investigated by isolating bacteria from the rhizosphere of naturally-regenerating spruce seedlings collected from two ecologically distinct zones of British Columbia. After an initial spruce growth screening experiment, the six most effective seedling growth promoting rhizosphere bacteria were re-tested using a factorial design in which seed, soil, and bacteria from both locations were examined in all possible treatment combinations, including pasteurized soil. Depending on the treatment combination, seedling biomass accumulation was stimulated by up to 59% in response to bacterial inoculation. Seedling biomass was greater when spruce seed, soil and rhizosphere bacteria originated from the same geographic site in comparison with treatments in which at least one factor (seed, soil and/or bacteria) originated from the other site. Soil pasteurization negated this effect. However, seedling growth promotion relative to uninoculated controls did not depend on the use of conifer seed, soil, and rhizosphere bacteria collected from the same area.

43

RAPID, REPEATABLE DETERMINATION OF SOIL MOISTURE IN FOREST CANOPY GAPS USING TIME DOMAIN REFLECTOMETRY (TDR). Andrew N. Gray Oregon State University, Corvallis.

The accuracy of TDR for determining volumetric water content was evaluated for soils from four forest stands. The TDR system operates by measuring the dielectric constant within waveguides defined by parallel steel probes, making it a rapid, non-destructive, and repeatable method. Proven effective in agricultural soils, TDR has rarely been applied to heterogeneous forest substrates. Regressions developed from TDR measurement of gravimetric soil samples were accurate within .03 cm^3/cm^3 volumetric water. Some soil types required separate regressions. The TDR technique was able to detect differences in soil moisture patterns within and among canopy gaps of different sizes.

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EFFECT OF SALAL REMOVAL ON TREE HEIGHT GROWTH AND FOLIAGE N: A PRELIMINARY STUDY. C.M. Preston*, X.C. Chang**, and G.F. Weetman** *Pacific Forestry Center, Victoria; **University of British Columbia, Vancouver.

Salal (*Gaultheria shallon* Pursh.) competes with young conifer regeneration for N on old growth cedar/hemlock cutovers on northern Vancouver Island. To study the effect of salal competition on fertilizer N distribution and recovery in trees, microplots (1 m radius) isolated to 50 cm depth using plastic barriers were planted to western hemlock, western red cedar and sitka spruce. In half of these plots salal was removed by repeated clipping (treated) and in the other half salal was present as understory (control). $(^{15}NH_4)_2SO_4$ was applied at 200 Kg N ha^{-1} in April 1991. Results obtained show that salal removal caused a significant increase in tree height growth. The greatest increase was observed for western hemlock. Non-salal understory foliage (taken from control plots) had higher N concentration than salal foliage in July, 1991. This was reversed in November due to the evergreenness of salal, which takes up N throughout the year. Salal removal did not significantly affect first year tree foliage N concentration in June, August and November. N-15 enrichment in tree foliage appeared to be greater in control than in treated plots. We think this is a dilution effect and expect N-15 content in biomass to be greater in treated plots.

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INFLUENCE OF RIPARIAN VEGETATION ON MICROBIAL DEGRADATION OF HERBICIDES IN SOIL. J.A. Entry, W.H. Emmingham, Forest Science Department, Oregon State University, Corvallis, OR USA

The persistence of aromatic herbicides in the environment has generated much concern because of their tendency to bioaccumulate and because of their potential effects on human health.

The type of vegetation growing on a site has profound effects on the soil microbial community. Forest vegetation, through litter deposition provides a favorable environment for the development of a rich soil fungal community. The establishment of forest vegetation in riparian areas adjacent to agricultural fields has been suggested as a method to control nonpoint source pollution. Riparian areas growing forest vegetation have a soil ecosystem with higher microbial biomass than riparian areas that are currently used as pasture. Forested riparian areas have a soil ecosystem that resulted in higher atrazine and 2,4-D degradation than riparian areas in pasture. This study indicates that the alternative agricultural practice of forest ecosystems in riparian areas may substantially reduce the input of toxic herbicides applied to agricultural fields to lakes and steams.

45

OZONE IN WESTERN WASHINGTON FORESTS. Felix A Basabe, Huxley College, Western Washington University, Bellingham.

Ozone data from 16 ground sites and from 31 hours of aircraft measurements will be presented. Ozone measurements in forested areas from 1985 to 1988 were consistently higher compared to the upwind urban area. Phytotoxic ozone episodes were measured on several occasions at different sites during this period. Aircraft measurements taken in 1988 showed high ozone levels over several thousand square kilometers in western Washington and southwestern British Columbia.

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CLOUDWATER CHEMISTRY AT STAMPEDE PASS AND THE ALPINE LAKES WILDERNESS AREA. Linda Cuykendall and Tony Basabe, Huxley College, Western Washington University, Bellingham.

Cloudwater samples were collected at Stampede Pass and in the Class I Alpine Lakes Wilderness Area to determine if cloudwater chemistry at Stampede Pass was representative of cloudwater collected at Granite Mountain. A passive collector was used at both sites. All samples were analyzed for hydrogen, sulfate, nitrate, chloride, ammonium, calcium, magnesium, potassium and sodium concentrations. A total of 156 samples were collected from July-September, 1991. Sample pH ranged from 3.5-6.7. Nitrate and sulfate were the dominant anions. Events were not collected simultaneously at both sites however, the chemical composition of cloudwater at Stampede Pass was similar to that found in the Alpine Lakes Wilderness Area.

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WINDFALLS IN THE SIOUXON DRAINAGE, SOUTHWESTERN WASHINGTON, USA. Charlotte Pyle. University of Washington, Seattle.

In an extensive survey for forest blowdown in the Siouxon drainage, uprooted trees were more typically found along clearcut edges than along naturally occurring edges or in large blocks of uncut forest. High contrast edges (old growth/recent clearcut) were intensively sampled to determine the number and direction of windfalls relative to edge aspect and topographic position within the watershed. For each windfallen (uprooted) tree, species, crown class, distance from clearcut boundary, and root and soil conditions were noted. Edges facing southwest toward the prevailing winds had the greatest number of windfallen trees per decameter of edge. However, east-facing edges also had a high number of windfalls reflecting the intensity of winter storm winds from the east. True firs (Abies sp.) were uprooted in greater proportion than they occurred in the stands next to the clearcuts. A disproportionately low number of uprooted dominant and codominant trees may be attributable to the high proportion of true fir in the intermediate and suppressed crown classes. In general, blowdowns did not extend beyond 30 m in from the clearcut edge. Where they did surpass 30 m, the forest edge was heavily dominated by silver fir (A. amabilis), and the topographic position was conducive to blowdown as well. Overall, the interaction of both landscape and stand level factors is important for the placement of windfirm edges.

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ECOZONES OF THE NORTHWESTERN CASCADES. Jan A. Henderson, Robin D. Lesher, and David H. Peter Mt. Baker-Snoqualmie and Olympic National Forest.

Gradient modeling approaches were used to develop a landscape-level environmental gradient model for the Mt. Baker-Snoqualmie National Forest. The model depicts a meso-scale moisture gradient across the Forest. This gradient is affected by prevailing storm tracks from the Pacific, modified by orographic effects related to topography. The model uses the elevation and aspect of the lower boundary of the Silver Fir Zone in this area to generate a map of "ecozones" where the Silver Fir Zone boundary falls within $\pm$ 150 ft (~46 m) of zonal limits. Once depicted as a map, the ecozone model can be used to describe and analyze the distribution pattern of species and Plant Associations across the landscape. It can also be used as a layer in a Geographic Information System to help map Vegetation Zones and Plant Association Groups.

49

PREDICTING THE LOCATION OF RECREATIONAL-CAUSED FIRES IN SLAVE LAKE PROVINCIAL FOREST, ALBERTA. Cristina Vega Garcia, P.M. Woodard, University of Alberta, Edmonton, B.S. Lee, NoFC Forestry Canada, Edmonton.

Recreation-caused wildfires are common in Alberta. This is particularly true in Slave Lake Provincial Forest, where an average of $ 500,000 per year is spent on forest fires caused by people. In this presentation, we discuss how choice behaviour theory and site attribute information can be used to predict occurrence. We will outline statistical procedures to be used and show how neural net software may be applied to solve this problem. The approach represents a significant deviation from approaches currently being used.

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ENDANGERED, THREATENED AND SENSITIVE PLANTS OF FORT LEWIS MILITARY RESERVATION
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The occurrence of rare plants and their habitats have not been well-studied in the southern Puget Sound region. Fort Lewis Military Reservation covers 86,000 acres in southern Puget Sound province, of which 24,000 acres are non-forested, prairie and wetland sites. The objective of this study is to identify and delineate the location of rare plants and associated species, and describe and map their habitat. The Natural Heritage Program of the Washington State DNR have identified 19 sensitive plants and 1 endangered plant suspected to be found at Fort Lewis. Two of these rare plant species (Aster curtus and Trillium parviflorum) have been located at Fort Lewis, we will attempt to determine the occurrence of the remaining species. Information from this study will assist the Army in the protection and management of rare plants and their habitat.

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PRIMARY CAVITY EXCAVATORS IN MANAGED ABIES GRANDIS FOREST HABITATS IN WASHINGTON'S EAST CASCADES.
Kenneth R. Bevis Central Washington University, Ellensburg.

Cavity excavating bird species are important components of forest ecosystems. We examined how these species responded to timber management in one forest type under three management regimes: unmanaged, partial cut (shelterwood) and minimal retention (seed tree). We measured relative abundances of primary cavity excavators, snag densities and canopy closure. First year results (1991) suggest a relationship between snag densities and primary cavity excavator abundance and diversity.

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BARKING DAMAGE OF LODGEPOLE PINE K. Anré Friedmann University of Alberta, Edmonton, Alberta, Canada.

Damage to lodgepole pine (*Pinus contorta*) by the removal of bark by small animals is having a severe impact on the survival and productivity of stands near Hinton, Alberta. The objectives of this study are: to determine when during the year barking damage occurs, to determine the primary damaging agent (red squirrel [*Tamiasciurus hudsonicus*] or snowshoe hare [*Lepus americanus*]), to determine if trees with previous damage are more susceptible to future damage and to determine if damaged areas have predictive physical or vegetative characteristics. Sixty-three plots were visited bi-weekly, and checked for new damage from the end of May until the end of August. Damage began in early June and continued through July. Eighteen percent of the trees surveyed were subject to new damage, while 49% of previously damaged trees were re-damaged. Contrary to previous beliefs the snowshoe hare is not the primary cause of this damage the red squirrel is. Timing, location, appearance and diameter of trees attacked need to be studied in order to correctly identify the cause of this type of damage. Analysis of tree and plot data is currently under way to find predictive characteristics.

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WINTER FOOD CACHING BY MOUNTAIN BEAVERS (*Aplodontia rufa*) IN A GIRDLED DOUGLAS-FIR STAND. J.P Farley and D.L. Campbell. USDA, Animal and Plant Health Inspection Service, Olympia, WA.

Girdling of basal stems and roots of Douglas-fir (*Pseudotsuga menziesii*) causes excessive tree mortality in managed plantations. Vegetation used by mountain beavers is being determined in a 15-year old stand with basal stem diameters of about 18 cm and canopy coverage of about 72% (SD 30%) near burrow systems prior to tree thinning. To locate food caches, 6 g radio transmitters were attached to sword fern bundles taken by mountain beavers. Cached vegetation recovered in February 1991 was compared with available surface plants within about 9 m of food caches of six burrow systems. Sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*) were the three major species of thirteen species recovered from food caches and were the dominant surface species. Respective percentages of food cache plants by weight vs ground coverage were: sword fern 34.9% (SD 25.4%) vs 36.4% (SD 20.0%); salal 32.4% (SD 20.0%) vs 47.7%, (SD 29.6%), and Oregon grape 8.5% (SD 9.5%) vs 31.8% (SD 35.0%). Percentages of sword fern and salal cached appeared closely related to their availability.

54

EFFECTS OF GRAZING ON HIGH ELEVATION SENSITIVE PLANT HABITATS IN THE OKANOGAN NATIONAL FOREST. Felix A Basabe, Huxley College, Western Washington University, Bellingham.

Rare plant meadow habitats were surveyed after 90 years of being grazed and again after six years of not being grazed. There has been an apparent increase in the occurrence of sensitive species in these habitats since grazing was halted. However, it appears that grazing was responsible for preventing forest encroachment on some of the sensitive plant meadow habitats. Light grazing may be required to maintain some of the sensitive species occurrences on rangelands.

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SETTING PLANT COMMUNITY PRESERVATION PRIORITIES: RESULTS OF A 16-YEAR CONSERVATION EFFORT IN WASHINGTON. Rex C. Crawford and Susan Trinh. Washington Natural Heritage Program, DNR, Olympia.

This paper discusses changes in protection priorities of plant communities listed in the Washington Natural Heritage Plan (WNHP). Plant community types indicate terrestrial ecosystems and used to assess the protection of and threats to common, native plant species in their natural habitats. Biennial up dates of the WNHP from 1983 to 1991 are compared with the initial conservation needs assessment in the 1975 federal "Yellowbook". Protection priorities of and preserves with plant communities are compared by province and zone within province. The increasing numbers of plant community types listed in WNHP reflects additional studies and the location of natural landscapes in the state.

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TAXONOMY AND CONSERVATION OF THE GRAPE FERNS AND MOONWORTS (GENUS BOTRYCHIUM) IN THE PACIFIC NORTHWEST. David H. Wagner University of Oregon, Eugene.

At present there are at least sixteen species of Botrychium in the Pacific Northwest, making it the largest genus of ferns in the region. Several have been named only in the past ten years and a few are still undescribed. Some are very rare and present challenging conservation problems, in part because of the difficulty in telling the species apart. Ongoing field research is helping to clarify the boundaries between the species, characterize their ecology, and add to our knowledge of the species' distribution. It is now possible to provide a pictorial summary of the genus and discuss the critical features which are used to distinguish the species. Research based guidelines for ethical, non-damaging specimen collecting are being developed. Specialized pressing methods, which assure the greatest amount of morphological data are preserved, are recommended.

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STATUS OF RARE PLANT INVENTORY AND PROTECTION EFFORTS IN WASHINGTON STATE. John G. Gamon. Washington Natural Heritage Program, DNR, Olympia.

Inventory efforts coordinated by the Washington Natural Heritage Program have resulted in the classification of over 250 native vascular plant taxa as Endangered, Threatened or Sensitive. More than 2500 occurrence records exist for these taxa. Federal lands have been more systematically inventoried than either state or private lands. Protection has been provided through agency policies, establishment of natural areas and voluntary landowner protection. However, most taxa occurring on private lands remain essentially unprotected. Future Washington Natural Heritage Program inventory and protection efforts should focus on taxa occurring primarily on state and private lands. Voluntary landowner protection is likely to be increasingly important for rare plant conservation.

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VEGETATION OF THE NOISY CREEK WATERSHED. Richy J. Harrod and Ronald J. Taylor, Western Washington Univ., Bellingham.

The vegetation in the Noisy Creek watershed, near Baker Lake, Washington, was described as part of a Endangered, Threatened and Sensitive (ETS) plant survey. A systematic search method was used to locate ETS plant species, to compile a species list and to qualitatively describe plant communities. Platanthera sparsiflora was the only ETS species found. However, 257 species of plants and 12 distinct plant communities were identified throughout the watershed. Plant communities were distributed in three major forest zones: Tsuga mertensiana/Abies amabilis, Tsuga heterophylla/Abies amabilis and Tsuga heterophylla/Thuja plicata. These forest types can be considered climax, or "old growth", based on age (ca. 750 years) and diversity of forest stands (multi-layered), species richness and soil composition.

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RARE PLANTS OF THE WENATCHEE MOUNTAINS, WASHINGTON. Richy J. Harrod, U.S.D.A Forest Service, Leavenworth, WA.

There are 51 plants which occur in the Wenatchee Mountains that are listed by the Washington Natural Heritage Program (DNR) as either Endangered, Threatened or Sensitive (ETS), and all listed as sensitive by the U.S.F.S Regional Forester. Many of these plants, such as Delphinium viridescens, Petrophytum cinerascens, Sidalcea oregana var. calva, Silene seelyi and Trifolium thompsonii, are strict endemics. Many known populations of these species and other ETS plants occur on National Forest lands. A general lack of information concerning the biology and ecology of these species makes it difficult for land managers to make appropriate decisions when timber sales or other projects occur within the vicinity of rare plant populations. Research and management must work closely in order to protect ETS plants by designing studies which meet management needs.

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RE-CLASSIFICATION OF FOREST AND HIGH ELEVATION RANGE HABITATS IN THE EASTERN NORTH CASCADES OF WASHINGTON. Therese Bielak and Tony Basabe Western Washington University, Bellingham.

The objective of this study was to develop vegetation classification methods for rangelands in the Winthrop Ranger District, Okanogan National Forest. Three methods were compared; a 0.75 inch hoop line-intercept method and two methods (plot and transect) using a 20 X 50 cm quadrat. Variability in habitat classification resulted from the use of these different methods. The hoop method tended to over estimate the importance of grasses and sedges.

61

PLANT SURVIVAL BENEATH 1980 TEPHRA FROM MOUNT ST. HELENS. D. B. Zobel, Oregon State University, Corvallis, and J. A. Antos, University of Victoria, Victoria.

Some subalpine forest understory shrubs, herbs and mosses survived at least eight growing seasons of burial in 15 cm deep volcanic tephra, deposited beneath intact forest in May, 1980. Tephra was removed from 50 m^2 of forest floor in 1980 and 1982, and 40 m^2 in 1987, to determine the size and number of buried surviving plants. Following 4, 28, and 87 months of burial, respectively, 6, 3, and 2 shrub species; 23, 16, and 1 herb species; and 12, 10, and 2 bryophyte species survived. Surviving after 87 months were Vaccinium membranaceum, V. ovalifolium, Erythronium montanum, Dicranum pallidisetum, and Rhizomnium glabrescens. Only V. membranaceum emerged from unexcavated tephra; in 1989, some recently emerged shoots were unattached to other shoots, and thus had survived burial for 5-9 growing seasons. Surviving buried plants may be an important but hidden source for delayed revegetation of some disturbed sites.

62

INVASION OF INDIGOBUSH (AMMORPHA FRUTICOSA L.) ALONG THE COLUMBIA AND SNAKE RIVERS, WASHINGTON AND OREGON. Richard R. Halse, Oregon State University, Corvallis, OR, and Judith B. Glad, Portland, OR.

Indigobush is a common component of riparian communities throughout much of the United States, but was not reported in the Northwest until the 1980s. It occurs along the Columbia River from the Hanford Reach to the mouth of the Willamette River on the Oregon shore and to Wahkiakum County on the Washington shore. On the Snake River, it has been found as far upstream as Garfield County, Washington, and Malheur County, Oregon. It has also been reported on the Umatilla River. It occupies the upper fluctuation zone of run-of-the-river reservoirs and the upper drawdown zone of storage reservoirs. The usual substrates are rock (including riprap) and sand. The species may have been introduced for erosion control or as wildlife food and cover. Fruits of indigobush are reportedly dispersed by wildlife, but there are indications that they can be transported by water as well.

63

STUDYING THE EFFECTS OF MUSHROOM HARVESTING ON CHANTERELLE PRODUCTIVITY IN OREGON'S MT. HOOD NATIONAL FOREST. Lorelei L. Norvell University of Washington, Seattle.

The choice edible *Cantharellus cibarius*, ectomycorrhizal with various forest trees, is an economically significant secondary forest product. In 1986 the Oregon Mycological Society (helped by the USDA Forest Service) initiated a ten-year study on whether or not chanterelle harvesting would adversely affect productivity or the growth of the mycorrhizal partners. Ten study plots were established in a 100-year old Hemlock-Douglas Fir stand in the buffer zone of Mt. Hood's Bull Run watershed. Since 1986, new chanterelles have been flagged by numbered skewers and mapped by triangulation with the dimensions of each fruiting body recorded every two weeks throughout the fruiting season. Since 1989 six of the ten plots have been harvested with chanterelles removed by cutting (3 plots) or pulling (3 plots). Four plots (in which no chanterelle removal is permitted) serve as controls.

Three years of harvesting data indicate that picking chanterelles does not have an adverse impact on subsequent chanterelle productivity over the short term. Additional observations suggest that canopy closure, annual mean temperature, precipitation, and the presence of coarse woody debris may be more significant in the productivity of a given chanterelle site.

64

VARIATION AND RELATIONSHIPS OF PLANT COMMUNITIES IN THE NORTH CASCADES. George Wooten and Peter Morrison.

Plant communities in the North Cascades Mountain Range of Washington respond dynamically to an extreme range of environmental factors. Vegetation types encompassing maximum spectral and geographic representation across the North Cascades were sampled and 1432 detailed plots were then selected to construct 261 composite samples. Detrended correspondence analysis on this data successively reduced by the elimination of outliers and obvious clusters resulted in a classification of minimally variant data sets. These data sets reveal details of plant community structure and facilitate environmental gradient analysis.

65

CLIMATE CHANGE AND SUBALPINE TREE GROWTH. David W. Peterson and David L. Peterson. National Park Service, C.P.S.U., University of Washington, Seattle.

Relationships between climate and annual growth were studied for Abies lasiocarpa, Picea engelmannii, and Larix lyallii growing near treeline in the North Cascades. Mixed- and single-species stands were sampled from ridgetop, midslope, and valley sites. Methods of dendroecology were used to relate variations in annual ring widths to seasonal climatic variables. Cold November temperatures negatively affect the following year's growth for all three species. A. lasiocarpa and P. engelmannii growth is promoted by cool, wet springs and low snowpacks. Growth of L. lyallii and P. engelmannii is positively correlated with early summer temperatures. The deleterious influence of snowpack is accentuated for trees growing on north-facing sites and in topographic depressions.

66

EFFECTS OF CLIMATE AND OTHER ENVIRONMENTAL FACTORS ON TREE ESTABLISHMENT IN SUBALPINE MEADOWS. Regina M. Rochefort and David L. Peterson, National Park Service, C.P.S.U., University of Washington, Seattle, WA.

Tree invasions in subalpine meadows of the Cascade Range occurred in the late 1800s and 1930s during periods of reduced snowpack and warmer temperatures. We studied spatial and temporal patterns of tree establishment in six subalpine meadows of Mount Rainier National Park and found distinct periods of invasion of Abies lasiocarpa in the mid-1980s. Spatial distribution is associated with herbaceous cover and topography. Temporal establishment is related to snowpack and warm temperatures. A warmer, drier future climate could allow more frequent periods of tree invasion and a directional change in the forest-meadow ecotone.

67

EFFECTS OF CLIMATE ON REGENERATION OF SUBALPINE FORESTS FOLLOWING WILDFIRE. Ronda L. Little and David L. Peterson. National Park Service, C.P.S.U., University of Washington, Seattle.

The influence of climate on subalpine conifer regeneration was examined on two large 90-year old burns northeast of Mount Rainier, Washington. We sampled 520 trees for age determination, and recorded microsite characteristics, soil type, herbaceous vegetation, and tree dimensions. Discrete peaks of tree establishment in the late 1950's, 1983, and 1989 were positively correlated with warm spring temperatures, and high summer precipitation, but were negatively correlated with high summer and fall temperatures. Establishment after wildfire may be faster and less periodic if springs become warmer, but these patterns may be offset by warmer and drier summers.

68

UNGULATE/FOREST RELATIONSHIPS IN OLYMPIC NATIONAL PARK: RETROSPECTIVE EXCLOSURE STUDIES. Andrea Woodward, Douglas B. Houston, Edward G. Schreiner, Bruce B. Moorhead Olympic National Park.

The effect of Roosevelt elk (Cervus elaphus roosevelti) on stand structure of old-growth Sitka spruce (Picea sitchensis) forests was evaluated by revisiting the sites of elk exclosures established ca. 1935 and ca. 1955 in Olympic National Park. Cover, morphology, growth and establishment of herbaceous, shrub and tree species were evaluated inside and outside of exclosures. Elk were seen to effect the growth and morphology of shrubs (e.g. Vaccinium spp., Rubus spectabilis), understory trees (e.g. Acer circinatum), and establishment of overstory trees (e.g. Tsuga mertensiana). We conclude that elk substantially influence the structure, and therefore function, of old-growth forests of the western Olympic Peninsula.

69

EFFECTS OF MINERAL DEFICIENCIES ON PHOTOSYNTHESIS OF SITKA SPRUCE SEEDLINGS. R.H. WAGNER UNIV. OF WASHINGTON, SEATTLE

Sitka Spruce seedlings were grown in sand culture in a greenhouse. Nutrients were supplied at three levels: low, medium, and "complete" (1/4 strength Hoagland-type solution). The low level was designed to induce "hidden hunger", a nutrient supply above the appearance of visible symptoms, but mild symptoms were visible at the low levels. During winter, artificial photoperiod and supplemental irradiance were used. Changes in the partial processes of photosynthesis were inferred from open gas-exchange system measurements. Light-response curves were used to obtain the net photosynthetic rate at light saturation and the photochemical efficiency from the slope at limiting light levels. Dark respiration was measured, and total leaf resistance to CO_2-transfer was calculated.

70

IN VITRO PROPAGATION, CALLUS INDUCTION, AND PROTOPLAST ISOLATION OF MELALEUCA ALTERNIFOLIA. Tze-Huey Wah and Hubertus Kohn. Western Washington University, Bellingham, WA.

The tissue culture potential of the woody Australian plant Melaleuca alternifolia was investigated. Shoot micropropagation with substantial bud proliferation was achieved on a soft (0.4% Agar) Shipton medium supplemented with 1 mg/l BAP. Rooting of propagated shoots was initiated on soft Shipton medium without hormones. Callus induction was attained only with shoot tip explants from in vitro grown plantlets on Shipton medium solidified with 0.15% Gelrite and supplemented with BAP (1mg/l), 2,4-D (0.2 mg/l), gibberellic acid (2mg/l) and three amino acids: 87 g/l glutamine, 26.6 g/l aspartic acid, 17.4 g/l arginine. Callus maintenance and growth was not successful on this or other media. Protoplast isolation from leaf mesophyll was only possible after extensive etiolation of leaves with gibberellic acid and dark treatments. Culture of protoplasts was not successful.

71

PLANT SPACE BEHAVIOR CONFIRMS W-WAVE HYPOTHESIS. O.E. Wagner. Wagner Research Lab., Rogue River, OR 97537

My work confirms that W-waves are important to plant organization (e.g. Nothw. Sci. 64:28-38). In space experiments (e.g. Ann. Revs. of Plant Physiol. 38:317-345) disorganization of growth of cells and other structures appears to be a typical effect of the microgravity environment. See book "W-Waves and A Wave Universe". From my experiments it appears that certain W-wave effects depend on the presence of a strong gravitational field and thus shapes, sizes, and spacings might be effected because of the lack of the appropriate W-wave patterns. Microscopic structures in cell components might also be changed. Long term stays in space might be impossible for any type of cell, including animal, without the presence of the hypothesized W-wave supporting gravitational field. Another possibility is that the space environment just disturbs the organization of the W-wave field without a gravity dependence and the microscopic structures of plants do not necessarily require a large g.

72

OTHER HARMONICS IN PLANT SPACINGS. O.E. Wagner. Wagner Research Lab., Rogue River, OR 97537.

I previously reported that many plant spacings represent harmonics of 1.6 Hz with other harmonics unidentified (Northw. Sci. 64:28-38). Apparently the 1.6 Hz harmonics are more associated with horizontal spacings while vertical spacings like distances between joints on Zea mays (2.4 Hz) represent harmonics of 0.6 Hz the reciprocal of 1.6. This was found for other plants with distances between 164 branch whorls of approx. 14 m ponderosa pines peaking at exactly 0.6 Hz with some minor peaks. Similarly 471 vertical spacings from Equisetum arvense revealed the most major peak at 8.4 Hz the 14th harmonic of 0.6 Hz while 315 spacings from Equisetum hyemale gave the most major peak at 5.4 Hz the 9th harmonic of 0.6 Hz. Plants like Lonicera hispudula vacillans give major peaks at harmonics of both 1.6 and 0.6 Hz like 8, 9.6, 12, 13.8, 16, 19.2, 32, and 48 Hz with a few peaks at, for example, 5 and 26.7 which are as yet unidentified with a definite harmonic series. See book "W-Waves and A Wave Universe".

74

THE PAST DISTRIBUTION AND CURRENT STATUS OF THE SPOTTED FROG *(Rana pretiosa)* IN WESTERN WASHINGTON. William P. Leonard Washington Department of Ecology.

Herpetologists in the Pacific Northwest noticed the decline of the spotted frog over 25 years ago. Spotted frogs once inhabited large areas of Western Washington. Today, they can be found in good numbers in the North Cascades and the northern portion of Eastern Washington. The cause of the decline is unknown, but introduced bullfrogs *(R. catesbeiana)* spiny ray fishes, as well as habitat loss, are among the leading theories. Western Washington museum specimens were examined to establish the historic range in Western Washington, and extensive field surveys were conducted between 1989-1991 to establish the species' current range. Whatever the reason, the spotted frog appears to be gone from most formerly known localities in Western Washington. In fact, there have been few verified sightings of the species in Western Washington since 1940. In 1990, a single spotted frog was found near Olympia. Attempts to find others there have so far failed. However this discovery renews hope that wild populations still exist in Western Washington.

75

DISTRIBUTION AND STATUS OF THE FISHER IN WASHINGTON. Keith B. Aubry U.S. Forest Service, Pacific Northwest Research Station, Olympia, Washington and Douglas B. Houston National Park Service, Olympic National Park, Port Angeles, Washington.

Our objectives were to determine the distribution of fishers (*Martes pennanti*) in Washington using sighting and trapping records, and evaluate their occurrence in relation to major vegetation and elevation zones. We obtained a total of 137 records from 1894-1991. Fishers still occur in the Cascade and Olympic Mountains and in portions of the Okanogan Highlands. They appear to be absent from the eastern edge of Puget Sound, the Kitsap Peninsula, the Willapa Hills, and the Blue Mountains. Fishers occupy different elevation zones east and west of the Crest. Western records were strongly skewed toward low to mid-elevations; 87% were at < 1000 m and the remainder were at < 1800 m. Only 30% of eastern records were at < 1000 m, and 18% were from 1800-2200 m. Most western records (54%) were from the Douglas-fir forest zone; remaining records were from the Pacific silver fir zone (26%) and the Sitka spruce zone (20%). Most eastern records (53%) were from the subalpine fir zone; others were from the Grand fir/ Douglas-fir (37%) and alpine zones (10%).

76

DISTRIBUTION OF PYGMY RABBIT (BRACHYLAGUS IDAHOENSIS) BURROWS IN SAGEBRUSH FLATS, WASHINGTON. Megan L. Gahr WACFWRU, University of Washington, Seattle.

In September 1991, a pygmy rabbit burrow survey was conducted in Sagebrush Flats, yielding a complete distribution and total count of burrow systems. Sagebrush Flats is the largest area where pygmy rabbits are known to occur in Washington State, and 75% of the area is leased for grazing. Active burrows were located in 1-ha units using a coordinate system. A total of 588 burrow systems were counted. The distribution of the burrows corresponded to three main drainage systems. The mean number of burrow systems per 1-ha plot was 1.6 in the grazed and 1.8 in the ungrazed portions. The total number was larger than known for the area based on a previous survey. The location of the burrows indicates that microtopography plays a key role in site selection. Burrows per unit area was similar between the grazed and ungrazed sections. This survey was the first step in a larger project to assess habitat use and population characteristics of pygmy rabbits in Eastern Washington.

77

DISTRIBUTION AND SPECIATION PROBLEMS WITH POCKET GOPHERS (Thomomys spp.) IN OREGON AND WASHINGTON. Gary Witmer. USDA Animal and Plant Health Inspection Service, Olympia, WA.

Pocket gophers are a distinct, specialized, subterranean mammal occupying much of western North America. In many areas, populations are controlled because of damage caused by feeding and burrowing activities. About 5 species and 20 subspecies are recognized in Oregon and Washington. Many small, disjunct populations are considered subspecies and some of these are being considered for federal protection by the USFWS. Distributions of these subspecies is poorly known with reliance on old records. Considerable intergrading occurs. Speciation has been in a state of flux partly due to the variation in morphological characters and poor understanding of the genetics and breeding relationships between species and subspecies. An effort is needed to delineate the range of species and subspecies and to provide criteria for reliable identification of live specimens in the field.

79

WASHINGTON STATE SHRUB STEPPE ECOSYSTEM STUDIES; WITH EMPHASIS ON AVIAN SPECIES OCCURRANCE, DENSITIES AND DIVERSITY. Frederick C. Dobler Washington State Department of Wildlife

Fifty five randomly selected sites in eastern Washington shrub steppe were surveyed in April and May, to determine the bird species composition of shrub steppe habitats. Three years of study with a total of 8,727 observations, recorded 94 species of birds. Four species, the western meadowlark, the horned lark, Brewer's sparrow and the vesper sparrow together made up over two thirds of the total observations. By contrast, 47 species were seen on three or fewer sample sites, and 38 of these species had three or fewer observations. Density was calculated for 18 species, including Brewer's sparrow, sage sparrow and sage thrasher, which had mean densities for all years combined of 0.63, 0.17, and 0.24 birds per hectare respectively, for the sites where they occurred. Comparisons of bird counts and plant species cover values showed a significant correlation between Shannon-Weaver indices of diversity.

80

STATUS AND DISTRIBUTION OF BALD EAGLES IN WASHINGTON. James W. Watson Washington Department of Wildlife, Mill Creek.

About half of the breeding and wintering bald eagles (Haliaetus leucocephalus) in the 7-state Pacific Recovery Area reside in Washington state. Most productivity and winter population goals for the state have been met; as of 1991 there are 444 nesting pairs, producing an average of 0.99 young per occupied territory, and stable to increasing wintering populations. Four of 11 sub-recovery zones within the state have not met recovery.

Habitat security remains the key to delisting the species. The majority of nests are on private land so efforts to protect habitat must be balanced with landowner rights, resulting in various degrees of protection. Goals for habitat security need to be established.

81

STATUS OF GREAT BLUE HERON NESTING COLONIES IN KING COUNTY WASHINGTON. Henning Stabins and Kenneth Raedeke, Raedeke Associates Inc., 5711 NE 63rd. Street, Seattle, WA. 98115

Field surveys and review of historical data were used to determine the current number of great blue heron nesting colonies and nests, and history of individual colonies. The number of heron colonies has increased from 4 in 1983 to 12 in 1990, with number of nests increased from 40 to 161. The number of nests was increasing in 6 colonies, and was stable in 2. No trend could be established in 3 colonies. One colony of 39 nests was destroyed by eagles in 1991. Average distubance free buffer area around the colonies was 49.8m (range 17 to 91m). Previous colony inventories noted loss due to direct harassment and shooting of herons. Colonies of less than 8 nests were most vulnerable to disturbance. Heron colonies are now increasing numbers and size, even with urbanization of their habitat, but face threats from the recovering bald eagle population in the region.

82

SPECIES COMPOSITION OF TWO OREGON CENTRAL COAST GULL (*LARUS* SP.) FLOCKS. Kathy Merrifield, Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, Oregon, 97331-2902.

Western, Glaucous-winged, California, and Mew Gulls (*Larus occidentalis, L. glaucescens, L. californicus,* and *L. canus,* respectively) were the major component species of gull flocks in the Yachats River mouth in 1990 and 1991 and at Ona Beach in 1990. Western Gulls were present in all months and usually constituted over 75% of each flock from December through September. Glaucous-winged Gulls were well-represented in all months and were most numerous from December through April, usually constituting less than 20% of total gulls. Mew Gulls reached maxima in December or January, usually constituting less than 20% of total gulls, and were absent from June through September. California Gulls were absent from Ona Beach but sporadic at Yachats from January through March. California Gull numbers increased gradually through the summer and sharply in the fall, reaching maxima constituting from 75 to 89% of the each flock total in October. Total gull numbers peaked in October, coinciding with California Gull maxima. More minor component species occurred at Yachats than at Ona Beach. Monthly average flock totals were similar in size and fluctuation between the two sites.

83

PRELIMINARY OBSERVATIONS OF NESTING RAVENS (*CORVUS CORAX*) ON SAN JUAN ISLAND, WASHINGTON. Linda T. Campbell, P.O. Box 1502, Friday Harbor, WA 98250.

A census of common ravens nesting on the 56 square mile island of San Juan, in the San Juan archipelago of northwestern Washington, was begun in the spring of 1990 and continued in 1991. Raven territorial behavior led the author to most nests, all of which were in coniferous trees. Data were collected regarding the forest habitat and the nest tree characteristics as well as on the behavior of the nesting ravens. Ten nests, seven of them active, were discovered in 1990, and ten active nests were observed in 1991. Further study will be necessary to determine the total nesting population of the island.

84

STUDIES OF THREE TRANSLOCATED POPULATIONS OF THE WESTERN FENCE LIZARD IN NORTHERN PUGET SOUND. H. A. Brown. Western Washington University, Bellingham.

Sceloporus occidentalis is the most common and widespread lizard in the western United States, but there are no studies on populations living in northwestern Washington. This study provides data on body size and growth in three introduced populations at beach habitats where this species does not occur naturally, and it is part of an ongoing study of population dynamics of the species in northern Puget Sound. The parent population (15 miles north of Everett, WA) was surveyed from May 1986 to October 1991 by mark and recapture techniques. In September of 1986 I transplanted 10 adults, 15 subadults, and 25 hatchlings to Clayton Beach (along Chuckanut Drive in Skagit County), but I did not find the lizards here again until May of 1990. With this discovery I made further experimental transplants of juveniles during May/June of 1990 to Clayton Beach and two other beach sites (Oyster Creek and Cherry Point). Clayton is successful, and the last two populations also produced hatchlings in October of 1991.

85

SENSITIVITY OF POPULATION GROWTH RATES TO LIFE HISTORY COMPONENTS FOR MEDIUM-SIZED MAMMALS. James G. Hallett, Washington State University, Pullman, Margaret A. O'Connell, Eastern Washington University, Cheney.

Identification of the demographic components that most strongly influence animal population dynamics is essential for understanding life-history evolution and for conservation and management. We compared aspects of the population dynamics of two species with similar food requirements, but very different life histories: Virginia opossum (Didelphis virginiana) and raccoon (Procyon lotor). These species were studied by monthly live-trapping and radio-tracking from June 1980 to December 1984 in a small watershed at the Conservation and Research Center, National Zoological Park, Front Royal, Virginia. Population structure and dynamics were examined by constructing age- and stage-classified matrix models for each species. The elements of these matrices were the fertilities and survival probabilities of females in each age or stage class. The matrices were analyzed to determine the relative importance of fertility versus survival on population growth. For opossums, first year survival and reproduction had the greatest effect on population growth. Survival of adults was generally most important for raccoons. Changes in demography were attributable to a rabies epidemic that affected only raccoons.

86

EDGE EFFECTS ON SMALL MAMMALS IN FOREST REMNANTS OF SW OREGON.

L. Scott Mills, Biology Dept., Univ. of CA, Santa Cruz, CA.

Edge effects operate in a species-specific fashion on a system of 16 small (0.5-10ha) forest remnants surrounded entirely by clearcuts. The abundance of Townsends chipmunks (Eutamius townsendii) and Trowbridge shrews (Sorex trowbridgii) show no spatial trends across these forest remnants. However, capture rate of red-backed voles (Clethrionomys californicus) decreases from the interior to the forest/clearcut edge, while deer mice (Peromyscus spp.) show the opposite trend. While neither log volume, log abundance, soil moisture, or light levels relate to distance from the edge, soil temperatures do correlate with the vole and deer mouse edge effects. This abiotic factor, in conjunction with changing food abundances, may explain differences in species responses to forest edge.

87

LOG USE BY CALIFORNIA RED-BACKED VOLES.

David A. Tallmon and L. Scott Mills

Biology Dept., University of California, Santa Cruz.

Although trapping data have associated the California red-backed vole (Clethrionomys californicus) with downed logs, no radiotelemetry work has examined this relationship. On a forest island in Southwest Oregon we radiotracked four voles and mapped the locations of logs within the home ranges of each vole. On average, 97.8% of vole locations coincided with logs even though logs covered only 11% of the estimated home range area. This high use of logs during both resting and activity periods suggests that downed logs are important for foraging and nesting activities.

88

HYPOGEOUS SPOROCARPS IN MANAGED AND UNMANAGED FORESTS OF SOUTHWESTERN OREGON: COARSE WOODY DEBRIS- FUNGAL- SMALL MAMMAL INTERRELATIONSHIPS. David A. Clarkson, Marlboro College, Vermont. L. Scott Mills. Michael P. Amaranthus. Jennifer Ramstetter. Four old-growth forest fragments and clear-cuts abutting two fragments were sampled to address three questions: 1). does truffle abundance differ between forest fragments and clear-cuts?; 2). do logs increase truffle abundance?; 3). does the presence of truffles increase chances of locating California red-backed voles, Clethrionomys californicus? Two forest fragments had 20-40 times more truffles than clear-cuts. Truffles were four times more abundant under logs. Presence of truffles significantly increased the probability of locating voles. The data corroborate suggestions that coarse woody debris, hypogeous sporocarps, and red-backed voles are highly interdependent in both forest fragments and clear-cuts.

89

ABUNDANCES OF SMALL MAMMALS IN OLD AND YOUNG FORESTS ON THE OLYMPIC PENINSULA. Anne-Marie Gillesberg and Andrew B. Carey, Pacific Northwest Research Station, Olympia, WA.

We compared the abundance and diversity of small mammals occurring in old and young forests. Of particular interest were the patterns of abundance of Peromyscus and Clethrionomys, prey species of the spotted owl. Indices to summer abundances were obtained during 1987-1989 using snap trap transects in 6 old, and 8 young, stands. We caught 2596 mammals of 14 species; Peromyscus oreas, Clethrionomys gapperi, and Sorex trowbridgii were most abundant. Number of species did not differ between old and young forest. Neurotrichus gibbsii, S. monticolus, and P. oreas were the only species consistently more abundant in old forest than in young forest. Abundance of P. maniculatus did not differ among stand types. C. gapperi fluctuated in total abundance, and relative abundance between forest types, among years.

90

EXPERIMENTAL MANIPULATION OF MANAGED STANDS TO PROVIDE HABITAT FOR SPOTTED OWL AND TO ENHANCE PLANT AND ANIMAL DIVERSITY. William L. Kerschke and Andy B. Carey, U.S. Department of Agriculture, Forestry Sciences Laboratory, 3625 93rd Ave. SW Olympia, WA 98502

Since 1850 mature old-growth forests, of which the Spotted owl (Strix occidentalis caurina) is closely associated with, have been reduced by 70 percent. Through the use of silviculture and establishment of arboreal rodent nesting sites, we plan to accelerate the development of Spotted owl habitat in 50-60 year old second-growth forests by providing roosting and foraging habitat for owls, and to raise owl prey populations, especially flying squirrels. Sixteen study areas (8 ha each) were established in thinned and unthinned stands of timber at Fort Lewis Reservation. Sites were trapped prior to experimental treatments over a four week period during the fall of 1991 resulting in 119 Northern flying squirrels (Glaucomys sabrinus), 12 Douglas' squirrel (Tamiasciurus douglasii), and 3 Townsend chipmunks (Tamias townsendii). Prescribed treatments will take place in 1992. Populations will be sampled again in five years to determine success.

91

ECOLOGY OF THE WESTERN GRAY SQUIRREL (SCIURIUS GRISEUS) ON FORT LEWIS MILITARY BASE

Lori A. Ryan and Andrew B. Carey
USDA, PNW Research Station
Olympia, Washington 98502

The Western gray squirrel is a candidate for threatened status in Washington. Although limited information is available on this species, they have often been sighted in Oregon white oak (Quercus garryana). The range of the W. gray squirrel extends only to the northernmost range of Oregon white oak in Pierce County, Washington. Managers at Fort Lewis want to retain gray squirrel habitat. The objectives of this study are to 1) inventory and map habitat used by W. gray squirrel 2) observe squirrel food habits 3) estimate population densities and 4) explore relationships between Oregon white oak and W. gray squirrels. These findings will help in making management decisions on Fort Lewis.

92

NEST SITES OF NORTHERN FLYING SQUIRRELS IN MANAGED SECOND-GROWTH FORESTS. Todd M. Wilson and Andrew B. Carey, USDA, Pacific Northwest Research Station, 3625 93rd Ave. SW, Olympia, WA 98502

Northern flying squirrels (Glaucomys sabrinus)are the major prey of the Northern Spotted Owl (Strix occidentalis caurina). A telemetry study was initiated on squirrels to examine nest types and frequency of nest use. Sites consisted of unthinned and doubly-thinned stands of 50-60 year old second-growth forests. Some of the stands contained residual live trees and a high coarse woody debris component. Radio transmitters were attached to 31 squirrels and monitored throughout the winter and spring of 1991/92. Nest structures, height of nest site, nest use frequency, and distances between nests were recorded. Preliminary results showed an apparent high use of Douglas' squirrel stick nests; snag and live tree cavities were also used. In the future, the effect of residual trees and coarse woody debris on squirrel populations will be examined.

93

USING BIOTELEMETRY TO MEASURE MORTALITY SOURCES IN ELK. Jack L. Smith, Warren A. Michaelis, and Kreg Sloan, Washington Department of Wildlife, Olympia.

Helicopter darting was used to capture over 300 elk in four (4) Washington State elk populations. We used radio-collars and internal mortality sensor equipped radios. Animals were monitored weekly. Once a mortality signal was detected, field necropsies were performed to determine cause of death where possible. Other evidence at the scene including physical evidence, drag trails, parts of the animals removed or not removed, distance to the nearest driveable road was collected and recorded. A metal detector was used to examine each scene for evidence of method of kill (bullets or broadhead). This study is half finished with one and one half years remaining. We have to date captured over 300 animals and have investigated 86 mortalities. There are four (4) major causes of mortality. In order of the frequency of occurrence they are: legal take, poaching, wounding, and natural loss.

94

GLOBAL PERSPECTIVE ON ENDANGERED BRYOPHYTES. John A. Christy. Oregon Natural Heritage Program Portland.

Seventy-five researchers from 42 countries responded to a survey on global protection of endangered bryophytes, circulated to members of the International Association of Bryologists. Europe and Asia reported the greatest decline in species and ecological groups, with liverworts being more sensitive than mosses. The most endangered habitats are tropical forests. More than 60% of the respondents cited forestry as causing the greatest decline, with epiphytes as the most threatened ecological group. Alteration or loss of wetlands was the second most significant cause for loss of species. Only two countries outside of Europe have national lists of endangered bryophytes, although several provincial and state lists exist. More research is needed in the Pacific Northwest before we can answer these questions with any degree of certainty.

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DISTRIBUTION OF SOME COMMON FOREST LICHENS ON THE OLYMPIC NATIONAL FOREST. Robin D. Lesher and Jan A. Henderson. Mt. Baker-Snoqualmie and Olympic National Forest, USDA Forest Service.

Presence and abundance of lichens were recorded on 235 plots as part of an ecological inventory of the Olympic National Forest. The data were analyzed for distribution patterns relating to environmental and vegetative parameters, including elevation, ecozone (a moisture gradient), vegetation series and plant association. Common forest species include *Alectoria sarmentosa*, *Bryoria fuscescens*, *Hypogymnia enteromorpha*, *H. inactiva*, *H. imshaugii*, *H. physodes*, *Lobaria oregana*, *Sphaerophorus globosus*, *Platismatia glauca*, *P. herrei* and *Parmeliopsis hyperopta*. *Lobaria oregana* showed a tendency toward mesic and moist habitats, while other species such as *Bryoria fuscescens* and *Hypogymnia* spp. showed tendencies toward drier habitats.

96

USE OF LICHENS BY WILDLIFE IN NORTH AMERICA. Stephen Sharnoff Missouri Botanical Garden

A literature search was made for studies citing significant use of lichens by wildlife. Caribou (Rangifer tarandus) consumption of lichens was well documented. A number of studies judged lichens to be vital food in winter for two subspecies of black-tailed deer (Odocoileus hemionus sitkensis and O.h. columbianus), northern flying squirrels (Glaucomys sabrinus), and red-backed voles (Clethrionomys californicus and C. gapperi). Utilization by many other large and small mammals was reported to range from slight to seasonally important. In almost all cases, use was highest in winter. Some implications for forest ecosystems are discussed, and lichen use by birds and invertebrates is briefly summarized.

97

LICHEN REGENERATION FOLLOWING LOGGING IN CARIBOU WINTER HABITAT IN WEST CENTRAL ALBERTA. I.M. Snyder and P.M. Woodard University of Alberta, Edmonton.

This study investigates the effects of logging on terricolous lichen regeneration. Forty-five different-aged clearcuts, one 20-year-old partially-logged and three unlogged stands were sampled for all terrestrial plant species percent covers, post-logging treatments and environmental variables. Results show that lichens reach peak abundance in 20 to 30 year old cutblocks and remain constant thereafter in subalpine ecoregions, but decline after 20 years at lower elevations. Subalpine areas support more lichen overall. The partially logged stand contained the most lichens. Successional patterns in lichen genera are evident with Cladina and Cetraria reaching peak abundance in uncut stands. Although lichen abundance recovers to that of unlogged stands in 20 years, differences in species composition may affect utilization by caribou.

98

ECOLOGY AND SUCCESSIONAL STATUS OF TERRESTRIAL AND ARBOREAL LICHENS ON THE WINTER RANGE OF THE ITCHA/ILGACHUZ CARIBOU. A. R. Brulisauer and M. D. Pitt. University of British Columbia, Vancouver, B.C.

To assess the importance of recurring forest fires as a possible determinant of the open nature of forests that are rich in terrestrial lichens, we investigated the successional development of such stands. Lichen-rich stands of lodgepole pine (Pinus contorta) appeared to be self-perpetuating climax-communities, which in the absence of fire are able to maintain their typical open nature. Arboreal lichens were found to be governed by a combination of age and moisture which in turn influenced light conditions and self-pruning mechanisms. Cladina and Cladonia lichens were most abundant on well-drained and light intense stands. Cladonia species peaked at a stand age of ca. 150 years, whereas Cladina spp. continuosly increased with age.

101

CHANGES IN RELATIVE FREQUENCY OF EPIPHYTIC LICHEN SPECIES ON OAK AND ASH TWIGS IN WESTERN OREGON, 1971 TO 1991. Jan Palmer-Muller, Francisco J. Camacho, Stephen C. Sillett, and William C. Denison Oregon State University, Corvallis.

In 1991 we collected twig samples from Oregon white oak (Quercus garyana) and Oregon ash (Fraxinus latifolia) at fourteen sites in the Willamette Valley. These sites had been sampled in 1971 by the same methods. We recorded frequency and cover of all epiphytic lichens growing on five five-year-old and five ten-year-old segments at each site. We observed changes in relative frequency of some lichen species between 1971 and 1991. We now speculate that these changes in frequency occurred as a result of an increase in wet season concentrations of atmospheric sulfur oxides at the sampled sites.

102

DISTRIBUTIONS OF BRYOPHYTES AND LICHENS ON GARRY OAK TRUNKS. Michael W. Ryan University of Victoria, Victoria.

I examined the distributions of bryophytes and lichens on Garry oak trunks and possible factors influencing their distributions. On all trunks bryophytes were most abundant near the base, whereas lichens increased in frequency with height above the ground. Bryophytes occurred predominantly on the upper sides and lichens predominantly on the lower sides of leaning trunks, whereas both were distributed around all sides of straight trunks. Bryophytes and lichens showed no response to differences in the aspect of the trunk surface. Daily light levels, stemflow and direct interception were measured on several trees. Only direct interception showed a relationship to the distributions of bryophytes and lichens, with bryophytes inhabiting locations that intercepted more rain than those occupied by lichens.

103

NEW TRANSPLANT METHODS FOR EPIPHYTIC LICHENS. Chiska C. Derr and Bruce McCune. Oregon State Univ., Corvallis.

Ecological studies of epiphytic lichens may be enhanced by further development of simple, effective methods of transplant. Alectoria sarmentosa and Usnea longissima, pendulous, fruticose lichens, and the foliose Lobaria pulmonaria, were made into lightweight removable pendants and transplanted to original and new habitats. A 0.5 g tuft of Alectoria, 15 cm strand of Usnea or 0.2-0.4 g lobe of Lobaria was glued with clear silicone sealant to a 5 cm length of nylon monofilament with a 2 cm loop in the other end. Transplants were attached to tree branches using "Goody ponytailers", elastic loops with 1 cm plastic beads at each end and silicone coating the metal crimps. Reference standards for each species were used to correct weights to standard water content, eliminating differences due to humidity at the time of weighing. Standards of 1-5 g were oven dried to end metabolic activity, then equilibrated with ambient air during lichen pendant drying, and reweighed with each pendant weighing. Average growth over 4 months was 31% for Usnea and 4% for Alectoria. Methods are being tested to minimize fragmentation of Alectoria.

104

BIODIVERSITY OF THE SPECIES USNEA LONGISSIMA; TESTING FOR CHEMOTYPES AND DYE CHARACTERISTICS. Sherman G. Brough University of British Columbia, Vancouver.

Collections of the lichen Usnea longissima made in British Columbia and Washington were used to dye wool. Differences in dye colors were due in part to the dye methods used but that alone could not account for the wide range of colors obtained. Six chemotypes of U. longissima were detected through thin layer chromatography and these were related to the dye colors obtained. Progress on tests for predicting the chemical substances of the lichen and thus inferring their capacity to dye and the dye colors, is being developed for field use and permanent storage.

105

LIST OF NAMES IN CURRENT USE (NCU) IN CLADONIACEAE: A PROJECT TO AID IN STABILIZATION OF NOMENCLATURE. Teuvo T. Ahti, University of Helsinki, Finland

Proposals will be made to the XV International Botanical Congress 1993 in order to grant protection to listed names of plants and fungi in current use. Draft lists of generic names and, in some families, infrageneric names have been completed. The infrageneric list of the lichen family Cladoniaceae includes several names and typifications which are not tenable according to the present Code of nomenclature, but which can be maintained in use if the new proposals are accepted.

106

MULTIVARIATE ANALYSES OF ELEMENTAL CONTENT IN LICHENS OF OLYMPIC NATIONAL PARK, WASHINGTON. Fred Rhoades, Western Washington University, Bellingham, WA.

Thalli from six groups of lichens (*Alectoria sarmentosa*, *Bryoria* species, *Tuckermannopsis* species, *Hypogymnia* species, *Sphaerophorus tuckermanii* and *Platismatia glauca*) from the perimeter of Olympic National Park were analyzed for element content by Inductively Coupled Argon Plasma Spectroscopy. These lichens are exposed to gradients of atmospheric elements derived from marine, crustal and anthropogenic sources. Concentrations of elements assignable to each of these sources are highly correlated to others assignable to the same source. Each source's elements show different species-specific patterns across the various gradients. Factor analyses are used to summarize the data for groups of similarly-behaving elements and ordinate the lichen groups in multidimensional space. Discriminant functions of element concentrations correctly assign thalli to one of the six groups with high success.

107

A FLORISTIC SURVEY OF THE EPIPHYTE COMMUNITIES INHABITING THE CROWNS OF TWO OLD-GROWTH CONIFERS IN REDWOOD NATIONAL PARK, CALIFORNIA
Stephen C. Sillett Oregon State University, Corvallis
T. Scott Sillett Louisiana State Univ., Baton Rouge

We quantitatively sampled epiphyte communities inhabiting the crowns of two conifers, a coastal redwood and a Douglas-fir, in Redwood National Park. The trees, which were both about 600 years old and 78 meters tall, grew side by side on a ridge top within the Little Lost Man Creek Research Natural Area. We found 5 mosses, 2 liverworts, and over 20 macrolichens inhabiting their trunks, branches, and twigs. Canopy epiphyte communities were dominated by chlorophycophilous lichens and mosses. Three nitrogen-fixing lichens were encountered on a few branches in the Douglas-fir. Total epiphyte cover (%) was much higher on the trunk (41 vs. 1.5), branches (64 vs. 11), and twigs (46 vs. 14) of the Douglas-fir. Similarly, epiphyte species richness was higher on the trunk (15 vs. 4), branches (23 vs. 13), and twigs (7 vs. 5) of the Douglas-fir. Major differences in bark character and crown architecture between the trees probably contributed to differences in epiphyte communities. Unlike Douglas-fir, redwood bark exfoliates readily and consistently, exposing younger layers that are very smooth and hard. Redwood crowns also tend to be denser, narrower, and shadier than Douglas-fir.

108

VERTICAL SUCCESSION OF EPIPHYTES IN DOUGLAS FIR - HEMLOCK FORESTS
Bruce McCune, Oregon State University, Corvallis.

Epiphytes were sampled on branches and trunks of felled trees in three Douglas-fir-western hemlock stands in the Cascade Range, ages 95, 145, and 400+ years. Epiphytes were sorted and weighed in four functional groups: cyanolichens, alectorioid lichens, other macrolichens, and bryophytes. Biomass samples from throughout the crowns were integrated vertically and radially on individual trees to derive biomass density functions for each functional group. These groups colonize the forest in the same sequence through time as the order of vertical dominance in old growth, from top to bottom: "other" macrolichens (mainly *Hypogymnia* and *Platismatia*), alectorioid lichens (mainly *Alectoria sarmentosa*), cyanolichens (mainly *Lobaria oregana*), and bryophytes. It follows from these observations that functional groups of epiphytes migrate upwards in forests through time. For example, the *Hypogymnia* and *Platismatia* that dominate throughout young forests are found primarily in the upper canopies of old forests. Similarly, bryophytes enter a stand near the forest floor and gradually expand their dominance upwards.

109

PRELIMINARY OBSERVATIONS ON "ANTIQUE" FORESTS AND EPIPHYTIC MACROLICHEN DIVERSITY IN BRITISH COLUMBIA.
Trevor Goward University of British Columbia, Vancouver.

The results of field studies conducted in the Coastal Western Hemlock Zone and Interior Cedar-Hemlock Zone of southern British Columbia during the summer of 1991 suggest that "antique" forests older than 300-350 years support several lichen species absent from adjacent younger forests -- including "oldgrowth" forests aged 150-250 years. Such lichens tend to be either rare throughout B.C., or outside their range.

It is tentatively proposed that antique forests favour the establishment of rare lichens in three ways: 1) they offer a maximum number of microsites; 2) they provide a degree of environmental stability not present in most younger forest types, but requisite for colonization by at least some lichens; and 3) their longevity increases the likelihood of successful inoculation by random air-borne and animal-borne diaspores (the petri-dish hypothesis).

It is also proposed that whereas the long-term survival of many rather common lichen species in the Pacific Northwest may depend on the maintenance of oldgrowth forests, the survival of many rare lichens probably depends on the maintenance of antique forests.

Further work on this problem is in progress.

110

THE NOAA NATIONAL BENTHIC SURVEILLANCE PROGRAM DATABASE.
John T. Landahl, Environmental Conservation Division, NMFS, NOAA, Seattle, WA.

Since 1984, NOAA has conducted the National Status and Trends Program to study the environmental health of the coastal marine waters of the U.S. One part of this program is the National Benthic Surveillance Project (NBSP). This project has amassed a large database on levels of trace metals and anthropogenic hydrocarbon compounds in sediment and fish tissue, and on prevalence of disease and indicators of contaminant exposure in bottom-dwelling fish. Although the NBSP is a national program, the presentation will focus on the types of data available for sites on the West Coast. Data have been collected for 8 fish species (fourhorn sculpin, flathead sole, English sole, starry flounder, barred sandbass, hornyhead turbot, white croaker, and black croaker) from more than 40 West Coast sites. These data are available through the National Oceanographic Data Center (NODC).

111

STOCK IDENTIFICATION USING ELEMENTAL COMPOSITION OF FISH HARDPARTS

James N. Ianelli, Seattle, WA

Aspects on the methods, biology, applications and problems of using elemental composition of fish hardparts are reviewed. For stock identification purposes, these methods represent an alternative to conventional mark-recapture and genetic studies. The concept is based on the premise of detecting "natural tags" within hardpart structures, which reflect, to some extent, the environmental conditions and genetics of the stock. Such methods hold promise to resolve ambiguities encountered with other more traditional techniques. An international workshop of researchers active in hardpart elemental composition analyses was recently convened to review the limitations and potential of these methods. A summary of these findings are presented. An example application to a salmon stock identification problem is contrasted with results from investigations on the stock structure of a species of tuna.

112

STOCK IDENTIFICATION TECHNIQUES FOR SALMON ON THE HIGH SEAS.

R.V. Walker and K.W. Myers, Fisheries Research Institute, School of Fisheries, University of Washington.

For over 35 years U.S. scientists have used various methods to delineate oceanic distribution of North Pacific salmon and steelhead (Oncorhynchus spp.) and estimate intermingling of different stocks. These methods have included direct proof techniques (such as high seas tagging, coded-wire tagging, and freshwater parasites) and indirect estimation (such as scale pattern analysis, age composition, genetic methods, and trace element analysis). Strengths and weaknesses and examples from results of some of the methods will be presented. Tags have been used to define ocean ranges of salmonids from different regions in North America and Asia, while scales, which are available in larger numbers than tag recoveries, have been used for quantitative estimates of mixing of stocks. A parasite (Nanophyetus salmincola) acquired in Pacific Northwest freshwater has been used to identify North American steelhead in the North Pacific Ocean as far west as 163°E.

113

RNA/DNA RATIOS AS INDICATORS OF NUTRITIONAL CONDITION OF LARVAL WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*.

MICHAEL F. CANINO AND KEVIN M. BAILEY, Alaska Fisheries Science Center, NOAA, Seattle.

Food consumption and nucleic acid ratios of first-feeding pollock larvae in the Gulf of Alaska were sampled during early spring and mid-spring, 1989. A large patch of larvae was detected. Mean prey abundance, gut contents (prey larva^{-1}) and RNA/DNA values of larvae were higher within the patch than in areas outside the patch during early spring. By mid-spring, microzooplankton densities, feeding intensity and RNA/DNA of larvae both inside and outside of the patch had increased. The results indicate a linkage between food availability, feeding, and growth during early periods of larval development.

114

MANAGEMENT ADVICE FROM A SIMPLE DYNAMIC POOL MODEL WHEN STOCK-RECRUITMENT PARAMETERS ARE UNCERTAIN.

Grant G. Thompson, National Marine Fisheries Service, Seattle, WA

A simple dynamic pool model is used to examine the problem of stock-recruitment parameter uncertainty from a Bayesian perspective. Probabilities associated with different parameter values are used to weight the losses (i.e., opportunity costs to society) associated with any given fishing mortality rate. By choosing appropriate forms for the loss and probability density functions, the model is shown to result in an analytic solution. Because this solution gives the fishing mortality rate that maximizes the expected value of the logarithm of sustainable yield, it is denoted F_{MELSY}. The solution is a monotone decreasing function of parameter uncertainty, converging on the fishing mortality rate corresponding to maximum sustainable yield as the degree of uncertainty approaches zero. As an empirical illustration, the model is applied to the eastern Bering Sea stock of rock sole (*Lepidopsetta bilineata*).

115

THE SPAWNING DYNAMICS OF WALLEYE POLLOCK, THERAGRA CHALCOGRAMMA, IN SHELIKOF STRAIT, GULF OF ALASKA

Nazila Merati
NOAA-Fisheries
Seattle, Washington

The spawning dynamics of female walleye pollock, Theragra chalcogramma, in the Shelikof Strait, Gulf of Alaska were studied in 1990. The purpose of this study was threefold; first, to characterize spawning dynamics of this fishery. Secondly, to determine the age at first maturity in female fish. Lastly, to develop a immunochemical assay to assess reproductive condition and to test this assay against other more established methods to determine sexual maturity stage. At this time, an antibody to egg-yolk protein has been developed, native egg proteins have been characterized and an assay has been developed. The assay may be useful in distinguishing between immature and spent/recovering maturity stage. These stages are difficult to determine by visual inspection.

116

EVALUATING ANADROMOUS SALMON AND STEELHEAD CO-MANAGEMENT IN WASHINGTON STATE AFTER *U. S. v WASHINGTON*. Gilbert B. Pauley. Wash. Coop. Fish & Wildlife Res. Unit, Univ. of Washington, Seattle, WA.

A history of the 1974 case, *U.S. v Washington*, is presented. This case set forth guidelines by which anadromous salmon and steelhead from Puget Sound, Strait of Juan de Fuca, and Washington Coastal waters were to be divided between the treaty Indian Tribes and citizens of Washington State. In the early years following the case decision, the tribes and the state were highly adversarial and used different technical evaluation methods and data sets to present their positions in court. The Federal Court appointed a Technical Advisor to assist with this problem and reduce court time. As the tribes and the state began to co-manage the fish runs, the number of adversarial proceedings between them has declined dramatically.

117

Backman, Thomas. Columbia River basin salmon production.

A Salmon restoration program to maintain, restore, and enhance Columbia River basin salmon populations above Bonneville Dam by means of supplementation and hatchery reprogramming is described. The program is being developed in accordance with both sound scientific principles of conservation management, and applicable laws and regulations such as Endangered Species Act and the Pacific Salmon Treaty.

Supplementation is the stocking of genetically and ecologically compatible fish into the natural habitat to increase the abundance of naturally reproducing fish populations. Hatchery reprogramming is the changing of operations of existing salmon hatcheries to directly support the maintenance, restoration and enhancement of salmon runs above Bonneville Dam. Habitat restoration and protection are an important components of a salmon production program.

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PEOPLE VERSUS FISH: FLOOD CONTROL ATTITUDES AND POLITICS. Millard S. Deusen
Washington Department of Fisheries.

With increased flood damage occurring as a result of more frequent and larger flood events, a battle is brewing over the protection of fish habitat and the protection of private property. Have weak governmental regulations dealing with growth management finally caught up with us? Have the flood plains of our rivers and streams been encroached upon to the point of no return? Can fish and people co-exist or are the costs of flood control leaving no room for fish habitat? What is the attitude of people, the politics of flood control and how does the future look if flood hazard management does not include concern for instream resources. Washington's King County has taken a step toward addressing this situation through a draft flood hazard reduction plan. The Corps of Engineers has recognized the importance of instream resources and vegetation management. Will these efforts be too little too late or can they change the trend from "people versus fish" to "people and fish"?

119

WASHINGTON FISHERY ASSESSMENT INITIATIVE. **Rich Lincoln, Washington Department of Fisheries; Michael Grayum, Northwest Indian Fisheries Commission; Bob Gibbons, Washington Department of Wildlife.**

The management entities in Washington are beginning an initiative to identify and restore the region's depleted wild salmonid stocks. Under a coordinated approach, WDF, WDW and tribal staffs are beginning an effort that will: (1) complete and maintain a resource status review of the region's salmonid stocks; (2) identify stock production problems; (3) review current resource management objectives for wild and hatchery stocks; and (4) develop, implement, and evaluate integrated restoration programs for critical stocks. These restoration programs will provide an alternative to reacting to listing petitions under the Endangered species Act.

120

GLACIOLOGY, FROG FARMING, AND INFORMATION SHARING IN THE COLUMBIA RIVER BASIN.

Phillip B. Roger, Columbia River Inter-Tribal Fish Commission, Portland, OR.

Designing an inter-agency information sharing system presents challenges not described in classical systems analysis literature. An iterative process and flexible time lines are necessary to handle complex inter-agency problems. Conversely, system complexity offers unexpected opportunities for spin-off benefits. Success depends on trust, creativity, patience, and a sense of humor as much as on skilled analysts and programmers.

121

VISIONS OF A STOCK STATUS INFORMATION RETRIEVAL SYSTEM (SSIRS) Sandra M. Noble for the Wild Stock Action Team, U.S. Fish and Wildlife Service, Region 1, Portland, OR.

Difficult access to meaningful information concerning wild and naturally-reproducing fish stocks often frustrates the use of current, scientifically sound data in management decisions. The U.S. Fish and Wildlife Service (Service) proposes to bring on line an information system for 1) inventorying the status of wild and natural stocks, 2) identifying information gaps, and 3) expanding monitoring activities to address those "gaps". Use of the system will be shared among Service and non-Service fishery professionals and interested persons. Service personnel will work closely with their cooperators to obtain suggestions on system development, gain accurate data for the database, and develop cooperative monitoring programs. The Service envisions such a system as essential in assessing stock status, identifying and monitoring stock restoration projects, and providing the information needed to gain funding support for wild stock programs.

122

RIPARIAN COMMUNITIES IN WESTERN OREGON: THEIR STRUCTURE AND MANAGEMENT. Neil B. Armantrout, BLM, Eugene, Oregon

Riparian community composition and structure were recorded during stream and riparian inventories along streams managed by BLM in Lane County, Oregon. The level of intensity of inventory varied, but age and dominant species were recorded in all inventories. Three broad communities can be described, based primarily on past timber management. Unharvested areas are dominated by conifers, while clearcut areas are dominated by hardwoods. Streams where conifers were higraded have a mix of conifers and hardwoods. On some BLM lands, unaltered riparian communities may occupy as little as 3-5% of the total riparian acreage. Buffers, designed to protect fish habitat, do not maintain riparian communities. Proposed BLM riparian and stream management anticipates the restoration of conifer communities, but our observations suggest this will not happen without an active program of vegetation manipulation.

123

EFFECT OF HABITAT ENHANCEMENT AND CANOPY REMOVAL ON THE FISH COMMUNITY OF A HEADWATER STREAM R. E. Bilby and B. R. Fransen
Weyerhaeuser Co., Tacoma, WA

The riparian trees along a 2km section of stream in western Oregon were logged in 1985, in violation of forest practice regulations. As part of the judgement against the landowner, wood was placed in the channel to improve habitat in 1988. Fish populations and habitat have been monitored since 1986 at 3 sites: the enhanced area, an non-enhanced reach without a canopy and a non-enhanced reach with a canopy. Pool area increased 20% as a result of the wood addition at the enhanced site. Pool area during summer also increased at the site with the canopy due to beaver activity. Speckled dace (*Rhinichthys osculus*) have exhibited the greatest response, increasing in numbers at all 3 sites, with greatest gains in the enhanced reach. Salmonid density at all three sites also has increased since 1988. Age 0+ steelhead (*Oncorhynchus mykiss*) exhibit an inverse relationship between density and growth. However, no such relationship is evident between 0+ steelhead growth and dace density, suggesting that the two species are not competing for resources. Increased food availability, due to elevated autotrophic production, in the enhanced and non-enhanced, uncanopied reaches, and improved habitat in the enhanced and canopied reaches are the likely causes of the elevated fish populations.

124

PATTERNS OF COMMUNITY STRUCTURE AND MICROHABITAT USE BY STREAM FISHES IN THREE WASHINGTON STREAMS. David Lonzarich
University of Washington and Center for Streamside Studies.

Studies on the ecology of streams in the Pacific Northwest focus almost exclusively upon salmonids and have consequently biased our views of how these systems function and respond to land-use disturbances. An approach is advanced here that integrates information on the biology of other stream fishes with knowledge of salmonids to better evaluate the impacts of stream disturbance. Comparisons are made of fish assemblages in different streams examining relationships with habitat structure and flow regime. Further, potential inter-relationships among species are examined through studies of habitat and micro-habitat use. Seasonal electo-shocking and snorkeling surveys conducted in three Washington streams from summer 1990 to the present (including the major floods of winter 1990-91) reveal: (1) extensive spatial variability in assemblage and population dynamics and rapid recovery of assemblages even following major floods and; (2) variable but often strong patterns of habitat partitioning. Results for species associated with cover and pool habitats (i.e., coho salmon, speckled dace) will form the basis of experiments examining the role of habitat structure on inter-specific behavioral interactions.

125

DECLINING SURVIVAL RATES IN BRITISH COLUMBIA AND COLUMBIA RIVER HATCHERIES. Ray Hilborn, University of Washington, Seattle.

We review the hatchery output and adult production of chinook and coho hatcheries in British Columbia in the Columbia River basin. British Columbia chinook hatcheries have experienced very serious declines in survival so that total chinook catch has dropped in half in the last 15 years, despite a 5 fold increase in hatchery production. British Columbia coho hatcheries have seen less decline in survival, but the total catch has remained roughly constant (prior to 1991). Columbia River coho hatcheries have seen long-term declines in survival, but survival rates have stabilized in the last 5 years, likely due to a substantial increase in size at release. Columbia River chinook hatcheries have had highly variable survival, with good survival in the mid-1980s but very poor survival recently.

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SURVIVAL AND CONTRIBUTION RATES FROM PUGET SOUND AND WASHINGTON COASTAL HATCHERIES. Terry Wright, Northwest Indian Fisheries Commission, Olympia.

A Coded Wire Tag Retrieval and Analysis System (CRAS) was developed to analyze survival and fishery contribution data from tags released in Western Washington. Survival rates are demonstrated to be highly variable, both within a hatchery, between years, and between hatcheries. Regressions with survival and size or time of release as well as several other analyses available through CRAS explain some of this variability.

127
THE NOVEMBER 1990 FLOOD IN SOUTHWESTERN BRITISH COLUMBIA, AND OVERVIEW OF THE RESTORATION PROCESS. Robert Bland, C. Robert Bland Consulting Engineers, Vancouver, British Columbia.

The November 1990 flood caused widespread damage to rivers in southwestern British Columbia. Restoration works were assessed on a site-by-site basis by a team of engineers and environmentalists.

While a "people versus fish" conflict was evident, the team approach ensured that the restoration work was carried out with minimal environmental damage.

128
EMERGENCY FLOOD MANAGEMENT - OR THE BLANK CHECK APPROACH TO FISH HABITAT DESTRUCTION: A CASE HISTORY OF THE 1990-91 FIR ISLAND FLOODS. Brian Williams, Washington Department of Fisheries, Everett.

Protecting fish habitat during a flood event is oftentimes a difficult and thankless task. In the rush to relieve the sufferings of the flood victims, emotions, politics, and confusion drive the decision processes. Fish resources are expected to bear whatever burden is necessary to protect flood plain properties. Impacts to fish habitat are taken for granted. Fish resource managers are cast in the role of obstructionists. Regulatory permits that typically serve to protect fish life and fish habitat become paper exercises that translate into blank checks for fish habitat destruction.

We lost valuable fish habitat during the Fir Island floods. In the year following, hopefully we've recovered some of our losses. You be the judge.

129
CHANGES AND IMPROVEMENTS IN WASHINGTON SALMON CULTURE PRACTICES. Larry Peck, Washington Department of Fisheries, Olympia

The use of salmon hatcheries has been an intricate tool for achieving fisheries management goals in Washington State for nearly 100 years. Currently, the Washington Department of Fisheries (WDF) operates 58 hatchery facilities located throughout the state. Changes in WDF hatchery operations demonstrate the evolutionary nature of how, when, and what we do today at WDF hatcheries.

130
SALMONID ENHANCEMENT LESSONS FROM LARGE-SCALE PROGRAMS IN OTHER AREAS. Ken Bruya, Washington Department of Fisheries, Olympia.

In response to a directive from the Washington State Legislature, the Washington Department of Fisheries (WDF) recently developed a framework plan for doubling the state's salmon catch. One aspect of the plan was a review of the success of similar initiatives in Alaska, British Columbia, Japan, and the Great Lakes. There were valuable lessons learned from these initiatives that were incorporated into the plan developed by WDF.

131
ASSESSMENT OF AQUATIC HAZARDS FOR FROGS AT TULE LAKE AT LOWER KLAMATH NATIONAL WILDLIFE REFUGE USING THE FROG EMBRYO TERATOGENESIS. Robin Boyer, University of Washington, Seattle.

Decreasing overall species diversity at the Tule Lake and Lower Klamath National Wildlife Refuge has prompted a 2-year federally-funded investigation to assess water quality in relation to the indigenous communities. Agricultural fields, on which a variety of agrichemicals are utilized, border the refuge on three sides. These farms use refuge water, which is repeatedly recirculated between field and refuge, throughout the growing season. In the lab, the FETAX (frog embryo teratogenesis assay: Xenopus) model assessed water quality in reference to frog (Xenopus laevis) embryo mortality and malformation. Embryos were exposed to the undiluted field water of weekly samples collected from nine agricultural drainwater input locations at which the temperature, pH, dissolved oxygen, and conductivity were measured. Results indicate significant malformation and no significant mortality.

132
HABITAT USED BY SPAWNING AND REARING WHITE STURGEON IN THE LOWER COLUMBIA RIVER. Allen Miller and Michael J. Parsley, U.S. Fish and Wildlife Service, Cook.

We investigated habitat use by spawning and rearing white sturgeon (Acipenser transmontanus) in the Columbia River downstream from McNary Dam and quantified the available habitat. We measured water depth, mean column water velocity, and substrate at sites where we sampled for white sturgeon eggs, larvae, and juveniles. Spawning habitat was quantified using the Physical Habitat Simulation System and rearing habitat was quantified using a geographic information system. Depths, velocities, and substrates used by spawning and rearing white sturgeon differed markedly. Recruitment was positively related to discharge. The amount of spawning habitat in each area varied among areas and years, and was dependent on discharge. Impoundment has increased the amount of rearing habitat. Results will be used in formulating recommendations to mitigate the effects of hydropower development on white sturgeon populations in the Columbia River.

133
REPRODUCTION AND EARLY LIFE HISTORY OF WHITE STURGEON IN THE COLUMBIA RIVER BETWEEN BONNEVILLE AND McNARY DAMS. Calvin R. Sprague, U.S. Fish and Wildlife Service, Cook.

From 1987 through 1991, the U.S. Fish and Wildlife Service sampled white sturgeon (Acipenser transmontanus) eggs, larvae, young-of-the-year (YOY), and juveniles with "D" shaped larval nets and trawls in the lower three pools of the Columbia River. Catch per unit effort for all life stages varied among years and pools, and was highest each year in Bonneville Pool. Spawning and rearing locations were identified for each pool. Spawning dates were back-calculated using egg and larval staging techniques. Sturgeon spawned between late May and mid-July at 12-19°C in tailrace areas. Spawning success was highest during high water years. Rearing occurred in deeper areas of pools downriver from tailrace areas. Ages were estimated and food habits examined for YOU, yearling, and juveniles. Principal food item for young white sturgeon was the amphipod Corophium sp. Study results will be used to help identify potential methods for protecting and enhancing white sturgeon populations.

134
IMPLEMENTATION OF THE NORTHERN SQUAWFISH SPORT-REWARD FISHERY ON THE COLUMBIA AND SNAKE RIVERS. Craig C. Burley, Washington Department of Wildlife, Vancouver.

The goal of this project is to reduce the predation mortality of juvenile salmonids (Oncorhynchus spp.) out-migrating through the Columbia and Snake River reservoirs. Northern squawfish (Ptychocheilus oregonensis) is a major predator on out-migrating juvenile salmonids. This project is one component of an overall program designed to remove 10-20% of the northern squawfish population annually in reservoirs between Priest Rapids Dam and the mouth of the Columbia River and between Hells Canyon Dam and the mouth of the Snake River. Sport anglers are paid a reward of $3.00 per northern squawfish 11 inches or longer. During May 24-September 22, 1991, anglers removed 159,162 northern squawfish. The average per unit effort for the season was 1.09 fish * angler^{-1} hour^{-1} This project is ongoing and will be implemented in 1992.

135
THE NOAA NATIONAL BENETHIC SURVEILLANCE PROGRAM DATABASE. John T. Lindahl, National Marine Fisheries Service, Seattle.

Since 1984, NOAA has conducted the National Status and Trends Program to study the environmental health of the coastal marine waters of the U.S. One part of this program is the National Benthic Surveillance Project (NB SP). This project has amassed a large database on levels of trace metals and anthropogenic hydrocarbon compounds in sediment and fish tissue, and on prevalence of disease and indicators of contaminant exposure in bottom-dwelling fish. Although the NBSP is a national program, the presentation will focus on the types of data available for sites on the West Coast. Data have been collected for eight fish species (fourhorn sculpin, flathead sole, English sole, starry flounder, barred sandbass, hornyhead turbot, white croaker, and black croaker) from more than 40 West Coast sites. These data are available through the National Oceanographic Data Center.

136
NORTHWEST ENVIRONMENTAL DATA BASE. Peter J. Paquet, Northwest Power Planning Council, Portland; Thomas E. Pansky, Bonneville Power Administration, Portland.

The Northwest Environmental Data Base (NED) began in 1984 as a cooperative effort by BPA, the Council, the four Northwest states, Indian tribes, and federal land management agencies to assess the significance of the region's rivers for use in the Council's Protect Area designations, System Planning, and BPA's regional hydropower supply estimates. The effort has resulted in seven detailed resource databases - anadromous fish, resident fish, wildlife, natural features, cultural features, recreational, and institutional constraints - and a network of over 1,000 experts in the seven resource categories. The databases cover all four states (comprehensive) and contain the same data elements for each state (consistent structure and content).

137
SALMON ESCAPEMENT INFORMATION SYSTEM. Greg Konkel, Washington Department of Fisheries, Seattle.

Annual escapement counts of Pacific Salmon and steelhead for more than 1,100 locations throughout the Pacific Northwest and Alaska were organized in a computer database. A common data format and coding system was developed for more than 26,000 escapement records obtained from a variety of published and unpublished sources. Programs were written which provide a means of displaying trends in spawning populations by individual stream, watershed, and by state and regional determinations.

138
EFFECT OF STOCKING DENSITY ON WILD AND HATCHERY-REARED CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA). C. F. Mazur and G. K. Iwama, University of British Columbia, Vancouver.

Stocking density is an important parameter when establishing optimal husbandry conditions for salmonids. This study investigated the effect of stocking density on the hematocrit, cortisol response, and survival of wild and hatchery-reared chinook salmon. Hatchery-reared chinook salmon had significantly lower hematocrit and plasma cortisol concentration increases as density was increased, compared to wild chinook. Equally accelerated mortality rates were observed for both groups of fish as density was increased. This study shows that increasing the stocking density of wild and hatchery-reared chinook salmon results in physiological changes and decreased survival.

139
SCIENCE, POLITICS, AND THE ENDANGERED SPECIES ACT. Philip Howell, Oregon Department of Fish and Wildlife, Portland.

The Endangered Species Act is in many ways the most powerful legislation affecting fish and wildlife. Congress will shortly be considering the act for reauthorization. This paper discusses how well the ESA is working, its strengths and weaknesses, possible scenarios for reauthorization, and the roles of biologists and fisheries management agencies in petitioning species for listing and administering the act.

140
THE USE OF THE ENDANGERED SPECIES ACT NOW AND IN THE FUTURE. F. Lorraine Bodi, American Rivers, Seattle.

The anadromous of the Pacific Northwest are in serious trouble, due to hydroelectric development, habitat degradation, overharvest, water diversion, and other causes. The Endangered Species Act is an important tool for the protection of these populations where other methods have failed. For example, the ESA is particularly appropriate in the Columbia River Basin where we have spent more than a decade trying to remedy low flows caused by hydroelectric and other development without success.

One challenge is to mesh the ESA with good science and policy so that we do not overload the system. Another challenge is to take action, erring on the side of the fish where data are uncertain. If we are to avoid new ESA petitions, the region will have to come up with an alternative approach that can accomplish the same objectives as the ESA.

141
SACRAMENTO WINTER CHINOOK: PROBLEM AND RECOVERY. Dave Vogel, CH2M Hill.

The Sacramento River supports a unique race of winter-run chinook salmon that has exhibited dramatic changes in spawning range and annual run sizes since the turn of this century. Although the winter-run experienced a large increase in numbers following the construction of dams (due to increased cold-water storage), a recent precipitous decline prompted Federal listing as a threatened species. The suspected reasons for the decline include water development, pollution, predation, loss of suitable spawning gravels, and recent adverse natural environmental conditions. There is some evidence that ocean fishery may also have adversely affected the run. A cooperative, multi-agency salmon restoration program was implemented prior to listing but was not timely or effective in preventing further declines in the winter run. Because of the small numbers of fish now returning each year, it is difficult for biologists to develop a comprehensive working knowledge of the run's biology, habitat, range, and relation to natural and man-made factors to evaluate how these factors may affect future existence of the run. The biological benefits and detriments of listing the winter-run chinook salmon are discussed along with recommended actions.

142
HARMFUL EFFECTS OF THE MARINE DIATOM (CHAETOCEROS CONCAVICORNIS) ON NET-PEN AND OTHER FISH IN PUGET SOUND. Jack Rensel, University of Washington, Seattle.

Blooms of phytoplankton have caused major losses in marine fish culture in Puget Sound and world-wide appear to be increasing in severity and geographic range. Although algal-caused mortality of fish is known to occur in net-pens, little is known about effects in natural and hatchery-reared salmon in Puget Sound. This paper focuses on the marine diatom Chaetoceros concavicornis and how it causes gill irritation and suffocation of mucus production that can lead to chronic stress response and death of salmon. Laboratory bioassay of Atlantic salmon showed blood-oxygen partial pressure was significantly reduced and blood-carbon dioxide partial pressure increased even at relatively low concentrations of the diatom. C. concavicornis blooms regularly in the fall in northern Hood Canal and apparently has caused mortality of migrating chinook salmon.

143

CAPTURE OF GRASS CARP FROM VEGETATED LAKES. S. A. Bonar, C. R. Bennett, G. B. Pauley, and G. L. Thomas, University of Washington, Seattle.

Seven techniques were evaluated for catching grass carp (Ctenopharyngodon idella) in five lakes containing aquatic vegetation. The methods included capturing fish with angling, pop-nets, or traps in baited areas; angling in non-baited areas; attracting fish to heated areas; and capturing fish using Asian methods which included lift nets and herding fish into gill nets. Herding fish into gill nets was the most effective of the techniques ($p < 0.001$), followed by angling baited areas. Herding is effective in lakes containing thick vegetation, submerged logs and other underwater obstructions, and might be effective for removing fish from overstocked waters or to monitor growth.

144

ENHANCING VEGETATION AND STRUCTURAL DIVERSITY BY MANIPULATING FOREST STANDS

Ted B. Thomas and Andrew B. Carey
USDA, PNW Research Station

The response of forest stands to silvicultural treatments to improve wildlife habitat is poorly understood. To ensure and maintain viable populations of endangered wildlife species it is neccessary to provide suitable habitat for these species and their prey populations. The objective of this study is to promote the development of suitable habitat for the Northern Spotted Owl (Strix occidentalis caurina). Young, managed forests at Fort Lewis Military Reservation will be silviculturally manipulated. Treatments will be applied to two 8 ha stands within 4 replicated blocks of 32 ha each. The blocks represent 2 stands with significantly different sizes of live trees (dbh and tree height) and amounts of coarse woody debris. The expected response to silvicultural treatments is to produce spatial heterogenity among the live trees and promote structural and species diversity in the understory. Forest stands of this age and structure will be intensively managed in future decades and it is important to recognize their potential as wildlife habitat.

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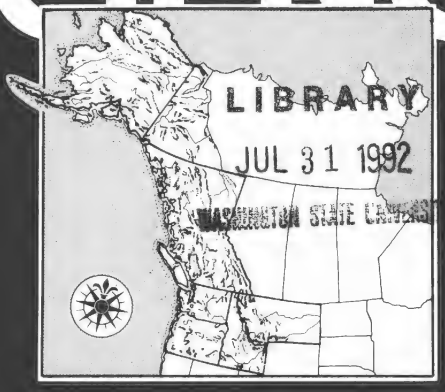

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Temporal, Spatial, and Size-Related Foraging of Wild Cutthroat Trout in Lake Washington

Abstract

We documented the feeding behavior of wild cutthroat trout *Oncorhynchus clarki,* a major piscivore, prior to the planned enhancement of juvenile sockeye salmon *Oncorhynchus nerka,* a potential prey species in Lake Washington. Food habits of cutthroat trout changed with body size, season, and time of day. Cutthroat trout ate invertebrates (*Daphnia pulicaria, Neomysis mercedis,* and various insects) until they reached a large enough size (generally when fork length is longer than 250 mm) to capture small fishes. Seasonal changes in the distribution of cutthroat trout corresponded with that of their primary prey, the longfin smelt, *Spirinchus thaleichthys,* when it was available. Juvenile sockeye salmon was a relatively minor constituent of the diet. Cutthroat trout appear to feed primarily in the littoral and upper limnetic zones, and respond to the diel and seasonal diffferences in accessibility of prey in these zones. This suggests that predation on juvenile sockeye salmon by cutthroat trout might increase in response to enhancement measures or to declines in the longfin smelt population.

Introduction

Temporal changes in prey distribution can influence the feeding behavior of a predator. Seasonal shifts in the abundance, availability, or vulnerability of prey are frequently reflected in a predator's diet. The diel feeding chronology of a predator might also be influenced by diel changes in prey distribution which can directly affect prey availability or vulnerability (Eggers 1977, 1978; Clark and Levy 1988). A description of the seasonal, diel, and ontogenetic changes in the food habits of a predator population is essential for determining the mechanisms of predator-prey interactions.

Cutthroat trout, *Oncorhynchus clarki,* are top predators in many lakes in the western United States. Lacustrine populations generally reside in littoral and limnetic habitats, and exploit fish and invertebrates commonly found in these zones (Idyll 1942, Trojnar and Behnke 1974, Andrusak and Northcote 1971, Nilsson and Northcote 1981, Hindar *et al.* 1988, Stables 1989). Little emphasis has been placed on the diel and seasonal variability in food habits of piscivorous cutthroat trout, however. In the present study, we examine temporal and ontogenetic shifts in the food consumed by subadult and adult cutthroat trout in Lake Washington, and relate this variability to temporal changes in the availability and vulnerability of prey.

The Washington Department of Fisheries plans to construct a spawning channel and/or hatchery to enhance the production of sockeye salmon (*Oncorhynchus nerka*) smolts. At maximum capacity, this facility is predicted to produce 110 million fry (Brannon *et al.* 1988) in addition to the natural river production (estimated to average around 30 million fry per year from 1978 to 1983; Beauchamp 1987).

Juvenile sockeye salmon and longfin smelt (*Spirinchus thaleichthys*) are the predominant planktivorous fishes in the limnetic zone of Lake Washington, and both are potentially important prey of cutthroat trout. A fourfold increase of juvenile sockeye salmon would increase their contribution to the limnetic planktivore community and could elicit a functional response (increased rate of predation with increasing prey density; e.g., Peterman and Gatto 1978) by piscivorous cutthroat trout to the juvenile salmon. Therefore, it is important to describe the current spatial-temporal patterns of predation as a reference for comparisons with the patterns from the expected increase in abundance of juvenile sockeye salmon during the enhancement program. Such a shift in prey selection by the piscivore might seriously compromise the desired goals of the enhancement program.

Study Area

Lake Washington is a large (88 km^2), monomictic lake adjacent to the city of Seattle, Washington,

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USA. The lake generally stratifies from April to October with mean (0-20 m) epilimnetic temperatures ranging from 8° to 16-18°. Further description of the lake and its fish community can be found in Beauchamp (1990). We partitioned the lake into five nearshore (0 to 15 m deep) areas and four offshore areas (from surface to bottom in areas deeper than 15 m), along the longitudinal axis of the lake (Figure 1). The Cedar River mouth and a 100 m area extending beyond the slopes of the river delta formed a 2 ha area designated as nearshore area five (Figure 1).

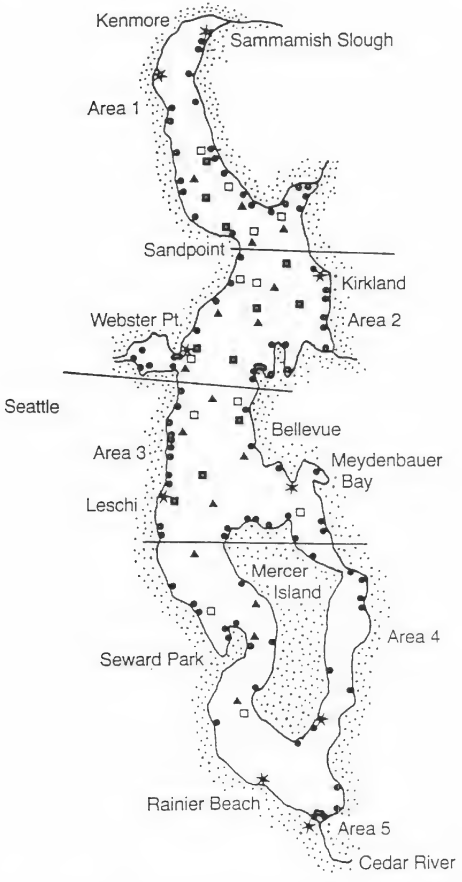

Figure 1. Lake Washington showing the locations sampled in 1984 and 1985. The lake was divided into five areas (delineated by horizontal lines) along its longitudinal axis. The Cedar River delta is area 5. Symbols follow: star, fixed location gill net sets in 1984 and 1985; solid circle, random gillnet sets in 1985; and purse seine sets in May 1985, solid triangle; June 1985, solid square; and September 1985, open square.

Methods

Sampling in the Nearshore Zone

The five nearshore zones were sampled with horizontal gill nets twice each month from January 1984 to June 1985. Two fixed sampling sites within each zone (one each on the east and west sides of the lake) comprised a sampling series in 1984. In 1985, one fixed site and two randomly selected sites were sampled per area during each sampling series. We set gill nets in the nearshore zone 318 times in 1984 and 182 times from January through June, 1985 (Figure 1).

Sinking horizontal gillnets were used for sampling both cutthroat trout and larger prey fish (i.e., yearling and adult longfin smelt, sockeye salmon smolts, yearling yellow perch *Perca flavescens* and peamouth chub *Mylocheilus caurinus*) in the nearshore zones. The nets were 33 m long and consisted of nine panels (3.7 m x 2.0 m) of randomly arranged mesh sizes (25 to 127 mm stretched mesh, in 13 mm increments). The nets were set at 0800-1100 hours and retrieved the next morning. The horizontal gill nets were deployed only in the nearshore zone, and were always set roughly perpendicular to shore. This procedure was repeated until all five areas had been sampled twice each month.

Offshore Zone Sampling

In 1984, we sampled the pelagic predator and prey populations monthly (January to October) in each of the five offshore areas with vertical gillnets. Nine single mesh-sized nets were fished simultaneously in each area for 24 h; the mesh sizes ranged from 25 to 127 mm stretched mesh, and changed in 13 mm increments. Only prey fishes larger than 80 mm were vulnerable to the smallest mesh size we used. We assumed that catches in these nets provided an approximation of the vertical distribution of fishes integrated over the 24 h set time.

Recognizing the limitations of the vertical gillnet data, we sampled with 3-m Isaacs-Kidd midwater trawl at night to document the nocturnal distribution of all sizes of the major pelagic prey fish whenever possible. The trawl was towed at 9.7 km/h for 10 min at depth, and tows were made at depths of 8, 15, 22, 30, 36, and 50 m (bottom

depth permitting) in each of the five areas. We recorded the catches of each fish species by tow depth, area, and time. The midwater tows were made in late March or early April in 1984 and 1985 by Washington Department of Fisheries personnel. We were able to do additional midwater trawling in September and November 1987, and November 1988. These latter midwater trawl samples were taken several years after collection of the cutthroat trout stomach samples, but the distribution patterns of prey fishes agreed well with those reported earlier by Dryfoos (1965) and Traynor (1973). Given the consistency of distribution patterns reported over a 22 year period, we felt justified in assuming that the summer and autumn vertical distribution patterns observed in 1987 and 1988 could be applied to the years of our study (1984-1985).

A 17.7 m purse seine vessel was chartered in May, June, and September 1985 to sample predators in the pelagic zone. Serial purse seine samples were collected roughly every hour from 1500 to 0500 hours on 14-16 May, from 1800 to 1100 on 13-14 June, and from 1100 to 2300 on 19 September (Figure 1). A stratified random sampling design was used, with samples proportionally allocated according to the surface area of the pelagic zone in areas 1, 2, 3, and 4. Each vessel deployed a large herring seine (600 m corkline, 37 m deep, 2.5 cm stretch mesh). Each circular set represented one unit of effort and the time at which the seine was pursed was designated as the set time.

Stomach Analysis

Sample sizes from 1984 were small due to our concern for conserving wild, reproductive fish (the population size was not known at the time), and because many of the stomachs, especially from spawning fish sampled in winter were empty (75% in 1984 versus 22% in 1985). However, after discovering that the annual catch of wild cutthroat trout was approximately 20 percent of that for stocked rainbow trout, *Oncorhynchus mykiss*, in our 1984 samples, we analyzed the stomach contents of all trout sampled thereafter. Although trends in the food habits of cutthroat trout were similar during both years, we emphasize the 1985 data here because of the larger sample sizes.

Cutthroat trout captured in purse seines were anesthetized with MS-222, measured, weighed, stomach-pumped, allowed to recover, and then released near the area of capture. Cutthroat trout captured in gillnets were killed to provide stomach samples for analysis of the seasonal nearshore diet composition.

We analyzed stomach contents from all captured cutthroat trout. Fish were measured (fork length to the nearest 1 mm) and weighed (nearest 1 g) before stomach contents were removed. Prey items were categorized as fish (identified to species whenever possible), zooplankton, Mysidacea (*Neomysis mercedis*), insects, and other invertebrates. Lengths of prey fish were measured, and dry weights (20 h at 80°C) for each prey category were recorded as a proportion of the total weight of stomach contents from each fish.

Results

Predation by cutthroat trout on their major prey changed significantly between nearshore and offshore habitats (Mann-Whitney U test, $P < 0.02$ for fish prey, $P < 0.02$ for zooplankton, and $P < 0.0001$ for insects). Similarly, predation patterns on most major prey varied among seasons (Kruskal-Wallis test, $P < 0.05$ for fish prey, $P < 0.01$ for insects, but $P < 0.15$ for zooplankton). Therefore, we stratified this analysis by season and nearshore and offshore habitat.

Temporal Changes in the Distribution of Cutthroat Trout and Prey

The seasonal nearshore-offshore occurrence of cutthroat trout generally corresponded with the seasonal distributions of its potential prey species. *Daphnia pulicaria* became abundant in the upper 20 m of the epilimnion during May and remained so through early to midsummer; minimum summer densities occurred in August or September, and a second period of high density coincided with thermal destratification in October (W. T. Edmonson, unpublished data). We caught longfin smelt in both nearshore and offshore gillnets during late autumn and winter, but only caught them offshore in spring and summer (Figure 2). The relatively high catches of longfin smelt during winter corresponded to a strong even-numbered year-class that spawned and died, subsequently leaving a weak, odd-numbered year-class of over-yearlings in the lake. Juvenile sockeye salmon occupied the limnetic zone except as fry entering or as smolts leaving the lake (Figure 2). Although cutthroat trout

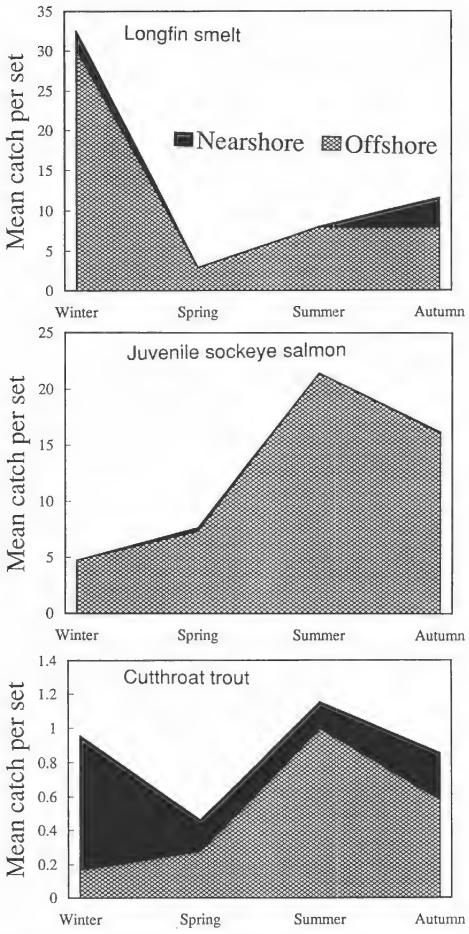

Figure 2. The seasonal nearshore-offshore distribution of longfin smelt, juvenile sockeye salmon, and cutthroat trout as indicated by the seasonal mean catch per set of horizontal gill nets nearshore and vertical gill nets offshore.

occupied both nearshore and offshore habitats throughout the year, more were caught offshore during spring, summer, and autumn, whereas the opposite was true in winter (Figure 2).

The diel vertical distribution of pelagic prey varied among species, but coincided with that of cutthroat trout at various times of the day. Pelagic cutthroat trout were most abundant at depths of 10 to 30 m in spring and summer with 55 percent of the catch between depths of 15 and 20 m both day and night (Figure 3). At night, the spring through autumn (April 1984, 1985; September, November 1987) midwater trawl catch of longfin smelt was highest at 8 m, whereas the catches integrated over 24 h in vertical gillnets indicated that longfin smelt remained deeper during the daylight and crepuscular periods (Figure 3). In contrast, the nocturnal catches of juvenile sockeye salmon were evenly distributed between 10 and 30 m in spring; in summer catches were highest between 22 and 30 m; and in autumn, nocturnal catches were highest between 30 and 50 m (Figure 4). Again, the 24 h vertical gillnet catches of juvenile sockeye salmon suggested that daytime and crepuscular distributions were generally deeper than those at night (Figure 4).

Food Habits in the Nearshore Zone

Winter-spring—Small cutthroat trout (150-250 mm) ate mostly invertebrates during winter and spring, whereas larger cutthroat trout ate mostly fish (Figure 5). The primary prey of small cutthroat trout was insects (mostly larval and pupal chironomids) during winter, and mysids and *Daphnia pulicaria* in spring. During both winters, large cutthroat trout fed primarily on longfin smelt and to a lesser extent on prickly sculpin *Cottus asper* (Table 1). In 1984, large cutthroat trout ate significantly more longfin smelt in winter (Kruskal-Wallis test, $P < 0.05$) when larger numbers of spawning adult longfin smelt were available than in spring (Table 1). When the spawning population of longfin smelt was small in 1985, there was no significant difference in the number of immature yearling longfin smelt eaten between winter and spring (Kruskal-Wallis test $P > 0.2$). A small number of juvenile sockeye salmon and yellow perch were found in the stomachs of large cutthroat trout during winter and spring in 1985 (Table 1).

Summer—Cutthroat trout shorter than 300 mm ate insects, *Daphnia pulicaria,* and mysids during summer in the nearshore zone. Larger cutthroat trout ate mostly fish, including juvenile sockeye salmon (24% of the stomach contents by dry weight), threespine stickleback *Gasterosteus aculeatus* (25%), and longfin smelt (1%; Table 1).

Food Habits in the Offshore Zone

During spring and summer, fewer *Daphnia pulicaria* (Kruskal-Wallis test, $P < 0.0001$) and more longfin smelt and total fish ($P < 0.01$ and

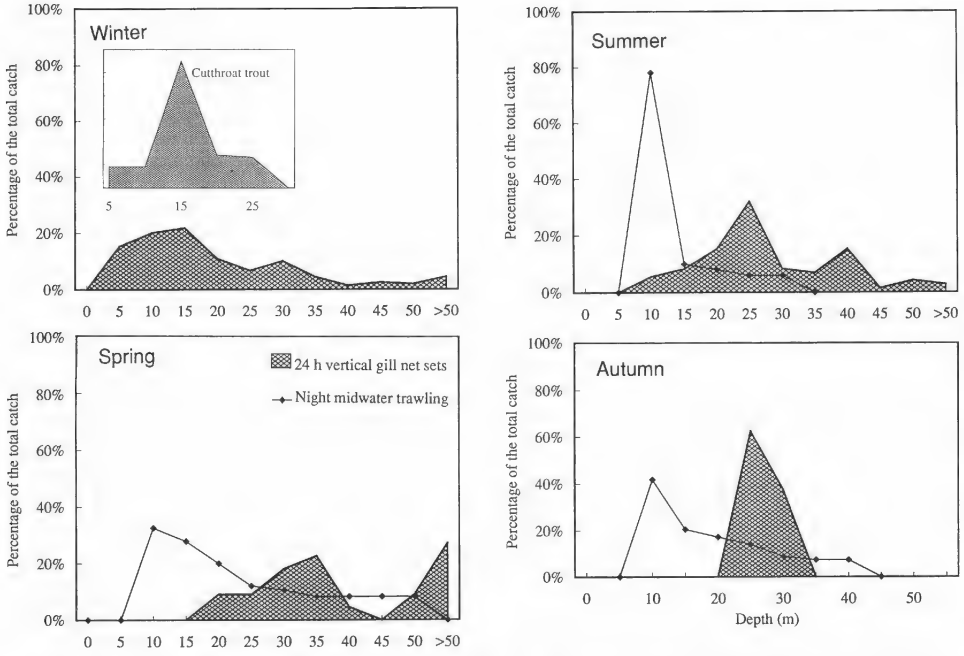

Figure 3. The diel vertical distribution of pelagic longfin smelt during winter, spring, summer, and autumn as inferred by the difference in depth distribution of the catches from vertical gill nets set for 24 h (1983-1985), and from midwater trawling at night (April 1984, 1985, September and November 1987, November 1988, and July 1989). The vertical distribution of pelagic cutthroat trout all year is indicated by the inset (depth scale of 5-30 m) in the top left panel.

TABLE 1. Percentage composition (by dry weight) of prey fish species in the diet of large (≥250 mm) cutthroat trout by season and habitat in Lake Washington. Species in the Other Fish column are identified as L = larval fish, S = juvenile coho or chinook salmon, Y = yellow perch, and are ordered from highest to lowest proportion of the stomach contents by dry weight.

Length Category (mm)	*N*	Longfin Smelt	Sockeye Salmon	Threespine Stickleback	Prickly Sculpin	Other Fish	Unidentified Fish
Winter 1984, Nearshore							
≥250	8	60	0	0	2	0	13
Spring 1984, Nearshore							
≥250	10	10	0	6	0	0	10
Summer 1984, Nearshore							
≥250	4	1	24	25	0	0	0
Summer 1984, Offshore							
≥250	4	0	23	9	0	16	25
Winter 1985, Nearshore							
≥250	28	24	2	0	4	4	36
Spring 1985, Nearshore							
≥250	37	8	2	0	1	5	21
Spring 1985, Offshore							
250-299	6	11	0	0	0	17 L	0
≥300	40	55	2	2	0	9 Y, S, L	14
Summer 1985, Offshore							
250-299	24	4	0	6	0	0	11
≥300	33	12	10	16	3	0	26

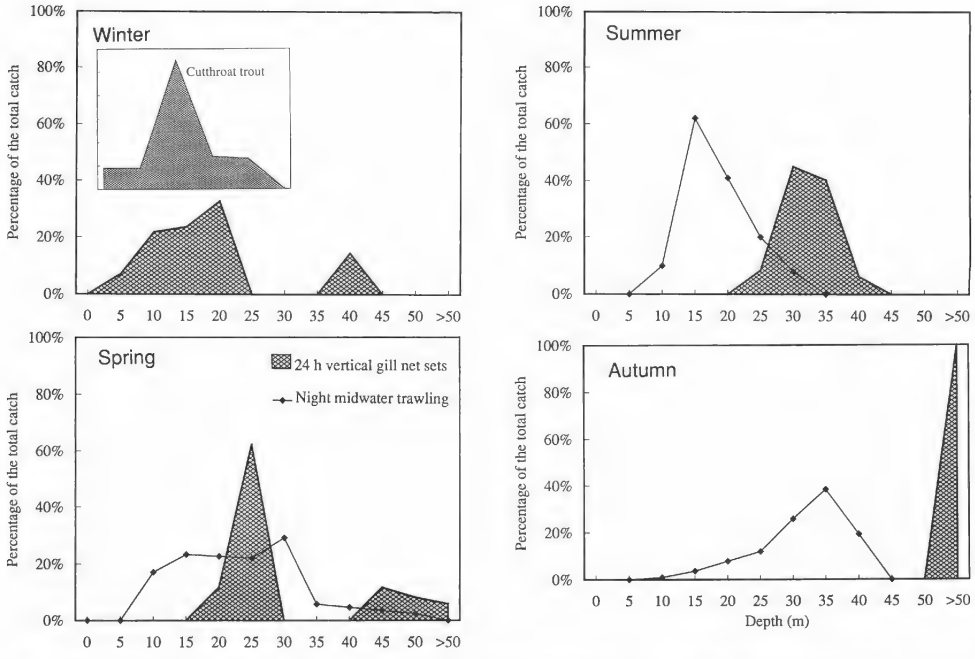

Figure 4. The diel vertical distribution of pelagic juvenile sockeye salmon during winter, spring, summer, and autumn as inferred by the difference in depth distribution of the catches from vertical gill nets set for 24 h (1983-1985), and from midwater trawling at night (April 1984, 1985, September and November 1987, November 1988, and July 1989). The vertical distribution of pelagic cutthroat trout all year is indicated by the inset (depth scale of 5-30 m) in the top left panel.

0.0001, respectively) were eaten as the size of cutthroat trout increased (Figure 5). During spring, cutthroat trout longer than 300 mm ate fish, primarily longfin smelt (Table 1), whereas *Daphnia pulicaria* and insects comprised less than a third of the diet (Figure 5). In summer, fish were still the predominant prey of cutthroat trout larger than 350 mm, whereas the contribution of daphnids in the diet declined with increasing predator size, and insects became a minor component of the diet (Figure 5). Threespine stickleback was the most important fish prey of large cutthroat trout in summer, followed by longfin smelt, prickly sculpin, and juvenile sockeye salmon (Table 1).

Diel Feeding Patterns of Pelagic Cutthroat Trout

The prey of pelagic cutthroat trout varied with time of day during spring and summer (Kruskal-Wallis test: $P < 0.005$ for longfin smelt, $P < 0.005$ for *Daphnia pulicaria*, and $P < 0.05$ for total fish prey; Figure 6). The weight of longfin smelt in the stomachs of cutthroat trout was greatest about 2 h after both sunrise and sunset, whereas the amounts of *Daphnia pulicaria* and juvenile sockeye salmon eaten were highest during daylight. The digestive state (He 1991) of the longfin smelt (bodies intact, some with small patches of skin missing) recovered from the peak feeding periods indicated that ingestion had occurred 0-2 h (at 15°to 17°) before the cutthroat trout were captured. Threespine stickleback were eaten both day and night.

Predator and Prey Fish Size

The size of fish eaten by cutthroat trout varied by season and species of prey ($P < 0.001$; two-way ANOVA; Table 2). Correlations between predator size and fish prey size were generally not significant except during the summer when the size of ingested longfin smelt showed a strong positive correlation with predator size ($r = 0.94$, $P < 0.02$; Figure 7). The size of threespine stickleback eaten showed a weak, but significant positive correlation

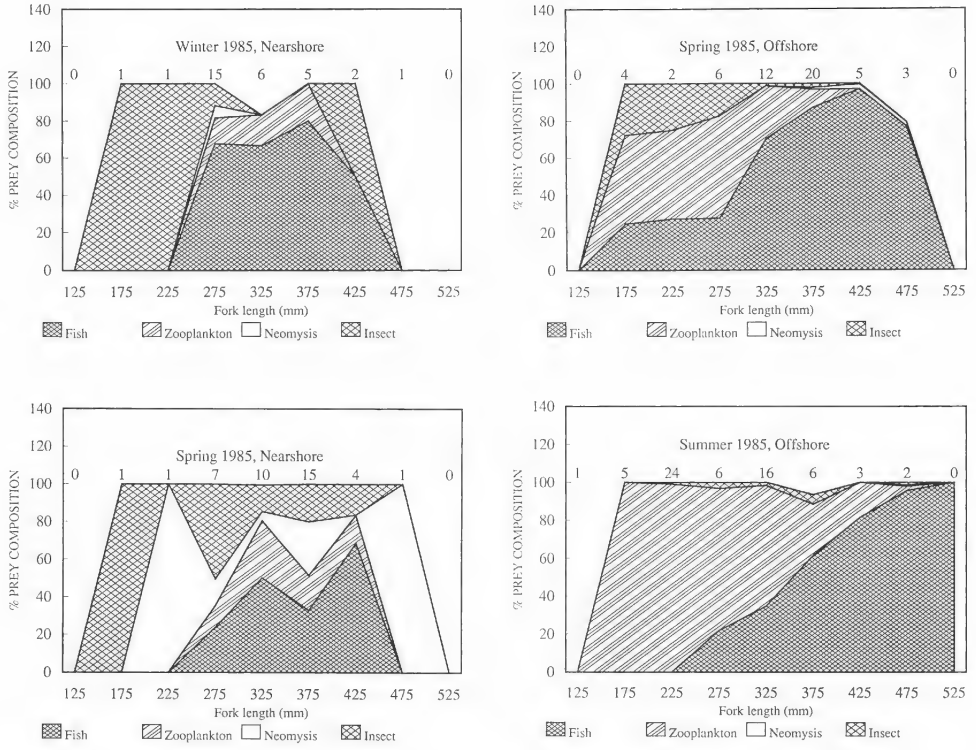

Figure 5. Percentage composition (dry weight) of fish, zooplankton (*Daphnia pulicaria*), mysids (*Neomysis mercedis*), and insects in the diet of all sizes of cutthroat trout in the nearshore areas during winter and spring 1985, and offshore during spring and summer 1985. Numbers indicate sample size for each 50 mm length interval.

TABLE 2. The mean length and SE of fish eaten by cutthroat trout during different seasons in Lake Washington.

Prey Species	n	Mean Fork Length	SE
Winter			
Longfin smelt	18	103	9
Prickly sculpin	3	83	1
Spring			
Longfin smelt	145	57	1
Prickly sculpin	3	29	1
Yellow perch	6	73	5
Sockeye salmon	37	26	1
Summer			
Longfin smelt	11	69	5
Prickly sculpin	31	37	2
Sockeye salmon	14	64	2
Threespine stickleback	71	36	1

with predator size ($r = 0.24$, $P < 0.05$), whereas size of the juvenile sockeye salmon eaten was not related to predator size ($r = 0.05$).

Discussion

The diet of cutthroat trout changed with body size, season, and time of day. Cutthroat trout ate invertebrates until they were large enough (generally larger than 250 mm) to routinely capture small fishes such as longfin smelt, threespine stickleback, prickly sculpin, and juvenile sockeye salmon. Luecke (1986) described ontogenetic shifts in the food of juvenile cutthroat trout in Lake Lenore, Washington, from zooplankton to larger benthic invertebrates, when the fish attained a length of 70 mm. Juvenile cutthroat trout in the Lake Washington drainage were generally 134-175 mm long before migrating from the natal stream into the lake (Scott *et al.* 1986). Hence, even the smallest

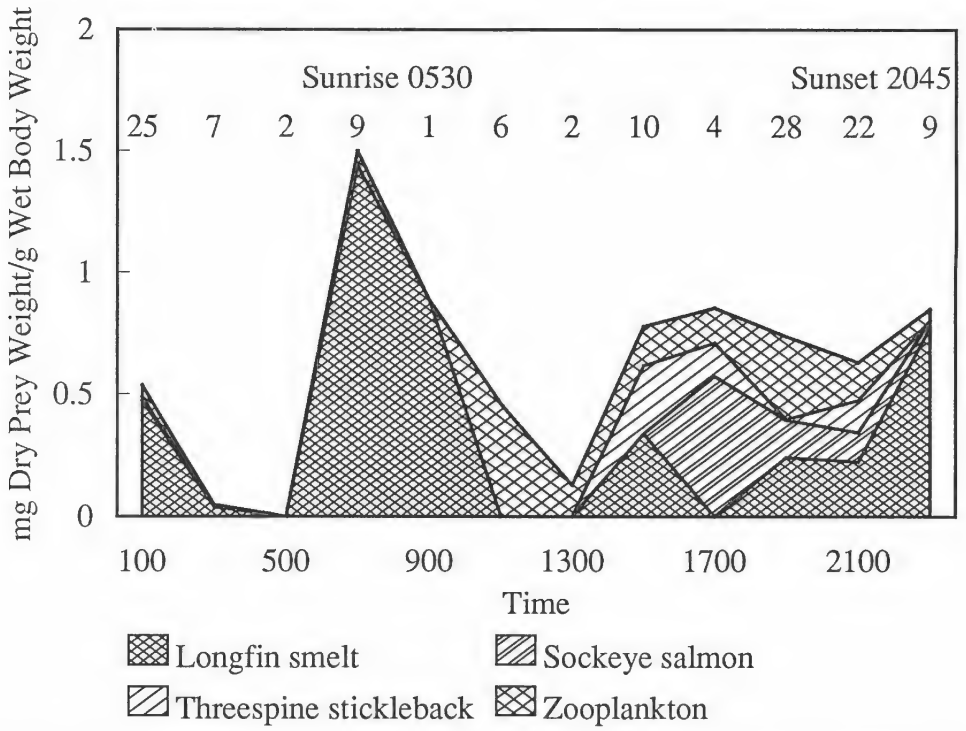

Figure 6. Diel consumption of major prey by cutthroat trout in the offshore zone of Lake Washington during May, June, and September 1985. Numbers indicate the sample size for each 2 h interval.

lacustrine cutthroat trout could utilize both zooplankton and other invertebrates (e.g., mysids and insects). When both invertebrate and fish prey are available, larger cutthroat trout could select zooplankton, benthic invertebrates, or fish. Shifts in prey composition might also be mediated by temporal changes in prey abundance and availability.

Longfin smelt was the primary prey of large cutthroat trout, as their distributions coincided throughout the year. Cutthroat trout occupied shallow to intermediate depths in the limnetic and littoral areas from spring through autumn, and concentrated more in the littoral zone at shallow to intermediate depths in winter. Longfin smelt occupied the pelagic zone from mid-spring through autumn; some longfin smelt resided in the limnetic zone in winter, but most moved to nearshore or profundal habitats (Traynor 1973, Beauchamp 1987). The nearshore prey community is in a state of flux during spring: adult longfin smelt die after spawning in winter (Dryfoos 1965), yearlings move offshore in mid-spring as the *Daphnia* populations increase, and warmwater fishes migrate shoreward. The cutthroat trout that remained in the nearshore habitat ate fewer longfin smelt, more invertebrates (particularly *Neomysis mercedis*) , and other fishes (e.g., yellow perch). However, most cutthroat trout appeared to move offshore in spring and continued feeding on longfin smelt.

Longfin smelt populations exhibit cyclic patterns of abundance (Dryfoos 1965, Moulton 1974), wherein even-numbered year-classes are typically 5 to 15 times more abundant than odd-numbered year-classes (Beauchamp 1987). Longfin smelt mature in 2 yr, spawn, and then die shortly thereafter (Dryfoos 1965); hence, this alternating cycle of low and high abundance is maintained. Although few cutthroat trout were sampled in 1984 when the abundance of longfin smelt was low, the data suggested that juvenile sockeye salmon became the predominant prey during the summer.

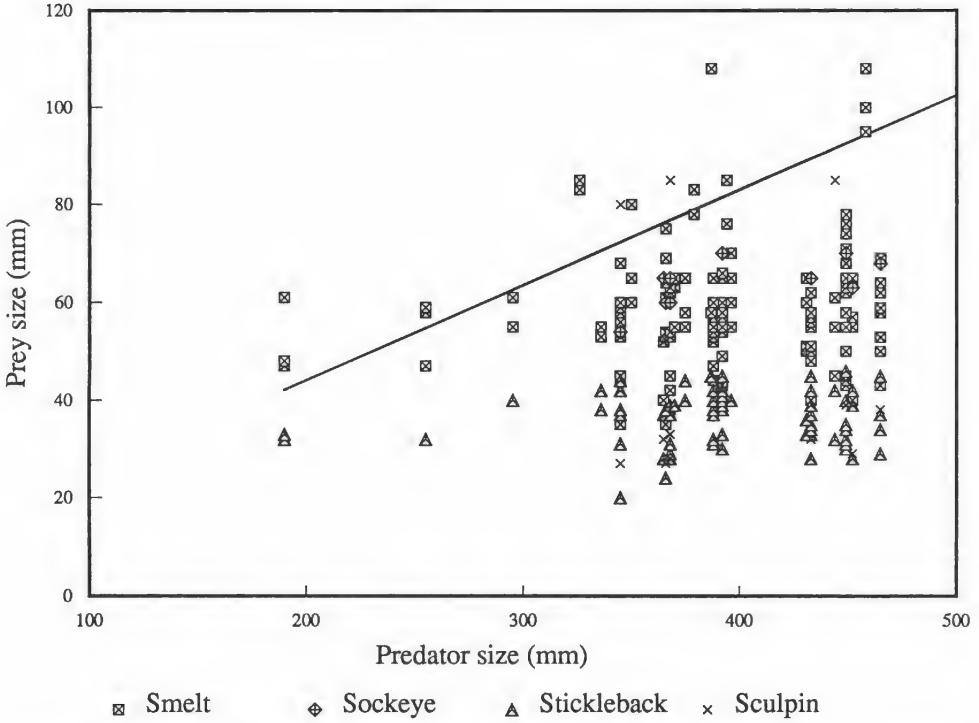

Figure 7. The relationship of predator size to prey size, pooled for all prey species and all seasons. The line indicates the only strong relationship which was between the size of piscivorous cutthroat trout and longfin smelt prey during the summer: (prey length) = 5.060 + 0.195 × (piscivore length), $r^2 = 0.86$, $N = 7$.

The diel pattern of predation by pelagic cutthroat trout on different prey corresponded with temporal changes in the vertical distribution or visibility of prey. Daphnids were abundant in the top 20 m of the water column during late spring, summer, and autumn (Edmondson and Litt 1982), and were eaten during daylight. Longfin smelt, which stay in deep water habitat during the day (Dryfoos 1965) were eaten during the crepuscular periods. Longfin smelt must pass through the depths occupied by cutthroat trout to feed in the upper epilimnion where uplooking predators benefit from the contrast between the silhouette of their prey and backlighting from the twilight sky.

When small planktivorous fishes occupy the lighted upper water column, they are vulnerable to sight-feeding predators (Eggers 1978, Beauchamp 1987, Clark and Levy 1988). Although we did not collect data on daytime distributions of pelagic prey fish, the differences between our vertical gillnet catches which integrated over 24 h periods and the discrete night-time trawl samples from later years are suggestive of the patterns observed by others. Dryfoos (1965) found that the median depth of yearling longfin smelt was 8 to 20 m deeper during the day than at night in summer and autumn. Eggers (1978) reported that individual juvenile sockeye salmon generally remained deeper than 40 m during the day, whereas those in schools foraged between depths of 10 and 30 m in summer and autumn. Threespine stickleback were rarely caught in midwater trawls during summer and autumn, but were often observed at the surface associated with floating mats of aquatic macrophytes and other debris in the pelagic zone.

Juvenile sockeye salmon were eaten only during daylight by pelagic cutthroat trout, but threespine stickleback were eaten during both day and night. During daylight, juvenile sockeye salmon

in Lake Washington remain in the deep limnetic zone or forage at intermediate depths using schooling as an antipredation strategy (Eggers 1978). Cutthroat trout might be able to locate schools of juvenile sockeye salmon at intermediate depths during the day when there is sufficient light for both piscivore and planktivore to locate their prey. Schooling behavior of juvenile sockeye salmon suggests that they are vulnerable to predation at these depths and times. The schools disperse at dusk when individuals might be less susceptible to predation than longfin smelt, which move higher in the water column.

The light threshold above which cutthroat trout can detect prey of a certain size probably influences their vertical distribution, and in turn, influences their diel shift in prey composition. Cutthroat trout in Loon Lake, British Columbia, could detect the copepod *Diaptomus kenai* (1.4-1.6 mm) below 30 m during daylight, but could not do so even at the surface between dusk and dawn; the sympatric Dolly Varden (*Salvelinus malma*) could still detect zooplankton all night between 5 m and the surface (Henderson and Northcote 1985). Inasmuch as the transparency of Lake Washington (Secchi disk transparency = 7 m) was slightly less than that of Loon Lake (8 m) in summer, the maximum depth of prey detection in Lake Washington would also be less. Cutthroat trout in the upper 20 m could feed on zooplankton during the day, and still have sufficient light to feed on larger prey like longfin smelt (50-130 mm) at dusk and dawn, when zooplankton were no longer detectable. Juvenile sockeye salmon would certainly be detectable in schools foraging at depths of 10 to 30 m (Eggers 1978) in daylight, but not when individuals were dispersed in deeper water. Since pelagic threespine stickleback appeared to remain near the surface, associated with floating cover, during summer and autumn, they would be vulnerable to predation by cutthroat trout at all times, and indeed were eaten both day and night.

An understanding of the spatial and temporal aspects of predator-prey interactions should help identify potential mechanisms of prey selection, and assist in identifying potential prey switching by cutthroat trout in response to the sockeye salmon enhancement plan. Our examination of the current foraging behavior of cutthroat trout will provide a valuable reference to compare to the predator-prey interactions during the enhancement program. The potential for predators to switch to the commercially and recreationally desirable sockeye salmon during years of low longfin smelt abundance has important implications for managing the fish community in Lake Washington. If a dramatic increase in the abundance of juvenile sockeye salmon, relative to longfin smelt and threespine stickleback, causes predators to feed selectively rather than opportunistically on sockeye salmon, then the resulting increased predation could seriously reduce the benefits expected from enhancing the sockeye salmon population.

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Habitat Use Patterns of White-tailed Deer, Umatilla River, Oregon

Abstract

Habitat use of white-tailed deer (*Odocoileus virginianus ochrourus*) along the Umatilla River in northeastern Oregon was investigated from January 1985 to July 1986. Twelve radiocollared deer were located 1148 times to determine habitat use. Plant communities used most in winter were dominated by Douglas hawthorn (*Crataegus douglasi*), ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and black cottonwood (*Populus trichocarpa*). A model predicted that 50 percent, 75 percent, and 95 percent of use would occur within 44 m, 99 m, and 248 m of cover, respectively, which obscured 90 percent of a standing deer. The majority of relocations occurred more than 1600 m from main roads. Retention of existing mature ponderosa pine-Douglas fir and cottonwood-ponderosa pine communities, and restriction of access to these areas in winter will help maintain white-tails in this area.

Introduction

White-tailed deer studies in the northern Rocky Mountains primarily represent areas of harsh winter weather, deep snowfall, and low temperatures (Mundinger 1981, Singer 1979, Pengelly 1961, Owens 1981). The winter weather patterns in the Umatilla River Basin are drier and warmer by comparison. Research in Oregon has been limited to the endangered Columbian white-tailed deer (Smith 1981, Suring and Vohs 1979). This study documents habitat use and forage use patterns for white-tailed deer in this area from January 1985 to July 1986. We also predict use relative to distance to effective hiding cover.

Study Area

The study area (75,300 ha) encompassed the northwestern foothills of the Blue Mountains in northeast Oregon, primarily on the Umatilla Indian Reservation (UIR). Elevations ranged from 335 m along the Umatilla River near Pendleton to 1325 m near Tollgate, Oregon, in the northeastern corner of the study area. This region is influenced by Pacific air masses, with hot, dry summers and cool winters. Annual mean precipitation is 31.0 cm at Pendleton, with most occurring in November, December, and January. Temperatures during the study period closely followed the 30 year monthly values. Precipitation was 7.7 cm in Jan-Mar 1985 including 32 cm snowfall in February, and 15.0 cm January-March 1986, with 37 cm snowfall in December 1985, compared with 30-year means of 10.7 cm precipitation and 20 cm snowfall during January-March.

Plant communities described by Bodurtha (1987) and Bell (1988) are listed in Table 1, along with the combinations and structural types used in analysis of habitat use patterns by deer. Riparian communities were dominated by black cottonwood, white alder (*Alnus rhombifolia*), ponderosa pine, Douglas fir, and black locust (*Robinia pseudoacacia*). The common shrub species included common chokecherry (*Prunus virginianus*), blue elderberry (*Sambucus cerulea*), common snowberry (*Symphoricarpos albus*), rose (*Rosa nutkana*), and Himalayan blackberry (*Rubus discolor*).

Upland plant communities include seral stages of the bluebunch wheatgrass (*Agropyron spicatum*)-Sandberg's bluegrass (*Poa secunda*), and bluebunch wheatgrass-Idaho fescue (*Festuca idahoensis*) habitat types. Dominant grass species were cheatgrass (*Bromus tectorum*), ripgut brome (*B. rigidus*), rattlesnake brome (*B. brizaeformis*), medusahead (*Taeniatherum asperum*), and Kentucky bluegrass (*P. pratensis*). The common forb species were western yarrow (*Achillea millefolium*), arrowleaf balsamroot (*Balsamorhiza sagittata*), mule's ear wyethia (*Wyethia amplexicaulis*), stork's bill (*Erodium cicutarium*), lupine (*Lupinus* spp.), and biscuitroot (*Lomatium* spp.).

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TABLE 1. Upland (Bodurtha 1987) and riparian plant community types and the associated pooled plant community and structural types used to analyze white-tailed deer winter habitat use in the Umatilla River Drainage, northeast Oregon.

Plant Community Types	Pooled Plant Community Types	Structural Types
	Upland Plant Communities	
Agriculture	Agriculture	Grass/Forb
Agropyron spicatum-Bromus tectorum *Agropyron spicatum-Festuca idahoensis* *Agropyron spicatum-Poa secunda*	Perennial Grass Communities	Grass/Forb
Bromus rigidus-Taeniatherum asperum *Bromus tectorum-Bromus brizaeformis* *Taeniatherum asperum-Bromus tectorum-Bromus mollis*	Annual Grass Communities	Grass/Forb
Rosa nutkana/Poa pratensis *Symphoricarpos albus/Poa pratensis* *Rhus glabra/Bromus rigida*	*Symphoricarpos albus-Rosa nutkana-Rhus glabra*	Low shrub
Crataegus douglasii/Symphoricarpos albus	*Crataegus douglasii/Symphoricarpos albus*	Tall Shrub
Physocarpus malvaceus/Symphoricarpos albus/Carex geyeri	*Physocarpus malvaceus/Symphoricarpos albus/Carex geyeri*	Tall Shrub
Pinus ponderosa/Holodiscus discolor/Symphoricarpos albus *Pinus ponderosa/Symphoricarpos albus/Carex geyeri* *Pseudotsuga menziesii/Physocarpus malvaceus*	*Pinus ponderosa-Pseudotsuga menziesii/Holodiscus discolor-Physocarpus malvaceus*	Mature/Shrub Mature
	Riparian Plant Communities	
Populus trichocarpa/Symphoricarpos albus-Prunus virginianus		Mature
Pinus ponderosa/Crataegus douglasii-Prunus virginianus		Mature

The major shrub-dominated communities generally occurred as narrow, irregular shaped patches, less than 10 ha (25 ac) in size, on north-to-east facing slopes, surrounded by grass dominated communities.

Bodurtha (1987) described 5 common forest communities: ponderosa pine / oceanspray (*Holodiscus discolor*), ponderosa pine / common snowberry, Douglas fir / ninebark, Douglas fir / common snowberry, and grand fir (*Abies grandis*) / twinflower (*Linnea borealis*).

Much of the lower elevations were planted to winter wheat, barley or peas. Grass and alfalfa hay were grown on small irrigated fields along the Umatilla River and McKay Creek. The study area is grazed by cattle, horses, and sheep.

Methods

Deer were captured using Clover traps (Clover 1956), V-panel traps (Lightfoot and Maw 1963), and a cannon net (Hawkins *et al.* 1968) and fitted with 164 mhz. radiocollars. Deer were relocated from the ground using a receiver and 2 element, H-shaped antenna using triangulation. The relocation error polygon (Heezen and Tester 1967) was reduced by visually observing each deer when establishing a location. When this was not possible without disturbing the animal, the deer was approached within approximately 50 m, as estimated by signal strength, topography and vegetation conditions, and monitored from a circular path at 90 degrees to the signal direction until a precise estimate of location was possible. Locations were recorded onto 1:15,840 black and white aerial photographs and transferred to 7.5 minute, USGS topographic maps.

Relocations were separated by at least one nocturnal period, to meet the assumption of behavioral independence (Dunn and Gipson 1977). Relocations were distributed from sunrise to sunset to

represent the diurnal behavior of each deer (Kammermeyer and Marchinton 1977). Deer were located in a predetermined sequence which was rearranged each time a round of relocations was completed to meet the assumption that the probability of detecting an animal in any part of its home range was proportional to the amount of time the animal spent in that area (Samuel *et al.* 1985). Relocations occurred during daylight hours.

At each relocation, topography, vegetation, and activity were recorded. Slope, aspect on slopes > 10 percent, slope position relative to the ridges and major drainages, and elevation were recorded from 7.5 minute USGS topographic maps. Activity was determined by visual observation or by monitoring the radio signal over a 1 minute interval (activity = irregular signal, inactivity = regular signal).

Hiding cover was defined as vegetation required to hide 90 percent of a standing deer at 30 m (Black *et al.* 1976). Distance to hiding cover was placed into 10 m classes using 1:15,840 black and white aerial photographs. A cumulative frequency distribution was generated for relocations in the 10 m classes up to 250 m. This cumulative distribution was fitted to a 2 parameter Weibull probability density function:

$$F(x) = 1 - \exp\{-(x/B)\}C$$

where B = scale parameter and C = shape parameter (Bailey and Dell 1973). This function is a general-purpose function which depicts a range of unimodal shapes, including a reverse J-shape or a mound-shaped curve, which the road-density information was expected to approximate. A least-squares non-linear regression was used to fit the observed distribution to the above model (Helwig and Council 1979).

Winter deer locations were recorded by plant community type and structural classes (Table 1). Winter locations were defined as those occurring in November-March, after migratory deer moved from or to known summer ranges. Structural classes included low shrub, over 1 m height; tall shrub, 1-3 m height; sapling/pole, < 53 cm DBH; mature/forest, > 53 cm DBH. Summer vegetation analysis was limited to structural classes.

Availabilities of each plant community and structural class used in winter were determined from the relative area occupied within 3 sampling units: the sample population study area (SA), 95 percent harmonic mean home range (HM) of each deer (Dixon and Chapman 1980), and core area (CA) within the harmonic mean home range (Samuel *et al.* 1985). The sample population study area boundary (43.6 km²) was defined to include all radio-collared deer and followed natural features which would limit deer movement, primarily large tracts of farmland. Sampling units were tested for differences in plant community availabilities using Quades's test (Conover 1980). Sampling units were treatments and plant communities were considered blocks. Only relocations lying within each sampling unit were used to determine deer use in each analysis. Plant communities, structural classes, and topographic components were delineated on 1:15,840 black and white aerial photographs, transferred to 1:24,000 USGS orthophoto quadrangles and area determined with a digital planimeter. The relative proportion of each parameter was determined within the sample unit. Availabilities for topographic components were measured only within the SA. Summer structural class availabilities were limited to HM because of the large range occupied by all deer during the summer. SA was 43.6 km², included home ranges of all radio-collared deer and was bounded by natural features which would limit deer movement, such as elevation or large tracts of farmland.

The heterogeneity chi-square test was used to test for differences in use of structural types between individuals using the null hypothesis that individual deer did not differ. Availability and use was based on the HM home range estimates. Expected values based on each deer averaged over 5.0, the minimum recommended by Roscoe and Byars (1971) for use in heterogeneity chi-square tests.

Data for individual deer were then pooled within HM and CA for tests comparing use to availability. A chi-square goodness-of-fit tested the null hypothesis that proportion of habitat use by all deer was equal to the proportion of habitat available, within a particular sample unit using a family alpha < 0.10. Simultaneous confidence intervals of use for each habitat were constructed using a Bonferroni test statistic (Neu *et al.* 1974). No expected values were < 1 and no more than 20 percent were < 5 for all chi-square tests (Zar 1984).

Roads were classified into 2 categories. Main roads had paved or gravel surfaces over 1.5 lanes wide passable to vehicles most of the winter (Thomas 1979). Seasonal roads over 1.5 lanes wide were not maintained in the winter. The latter road category was a combination of secondary

and primitive road categories (Thomas 1979). The distance from relocations to each type of road was categorized into 400 m intervals up to 1600 m. Road densities (km/km^2) were determined within HM home ranges. Deer with both summer and winter HM home ranges were used to test for differences in winter and summer road densities using a Wilcoxon signed ranks test (Zar 1984).

Results

Habitat Use

A total of 1,148 relocations was recorded from 12 individual deer. Of these locations 82 percent (n = 937) were used for winter and summer habitat use analysis, with 18 percent omitted because deer were disturbed. Summer relocations within HM totalled 466. Winter relocations totalled 471, 447, and 366 for SA, HM, and CA, respectively. Active behavior was recorded at 64 percent of the relocations during both summer and winter. Visual observations comprised 24 percent of summer and 42 percent of winter relocations.

Proportions of availability for community types were greater between sample units than proportions of use. Perennial grass availability decreased the most from the SA to the CA. Black cottonwood - ponderosa pine was absent from 3 HM home ranges, ponderosa pine - Douglas fir was absent from 2 HM home ranges, and ninebark - common snowberry was absent from 2 HM home ranges.

Winter use of plant community types differed significantly from availability within the 3 sampling units (Table 2). The agriculture type, perennial grass type, and annual grass type were used less than expected in all sampling units. Use of the Douglas hawthorne / common snowberry type and ponderosa pine - Douglas fir type was greater than expected. Black cottonwood - ponderosa pine was used greater than expected in SA and HM but was used in proportion to availability in CA. Availabilities of plant communities in winter were not different within the 3 sampling units ($P > 0.25$, Fig. 1).

Structural Classes

The use of structural classes within summer and winter HM varied from month to month (Fig. 2). Mature forest was the only class used consistently while use of all other classes was variable. Sapling/pole, and mature/shrub structural classes constituted less than 1 acre of the winter study area, and the low shrub structural class did not occur within the summer sample units.

TABLE 2. Goodness-of-fit chi-square test of use versus availability of plant community types by white-tailed deer during the winter of 1985-86 within the Umatilla River drainage, northeast Oregon. Availabilities are based on the relative area of each habitat within the sample population study area, 95% harmonic mean home range, and the core area. Simultaneous confidence intervals are based on a family alpha of 0.10. Plant community type names are PGC = Perennial Grass Community, AGC = Annual Grass Community, Syal-Ronu-Rhgl = *Symphoricarpos albus - Rosa nutkana - Rhus glabra,* Crdo/Syal = *Crataegus douglasii / Symphoricarpos albus,* Phma/Syal = *Physocarpus malvaceus / Symphoricarpos albus,* Pipo-Psme/Hodi = *Pinus ponderosa - Pseudotsuga menziesii / Holodiscus discolor,* Potr2/Syal-Prvi = *Populus trichocarpa / Symphoricarpos albus - Prunus virginianus,* Pipo/Crdo-Prvi = *Pinus ponderosa / Crataegus douglasii - Prunus virginianus.* Study area $\chi^2 = 501.2$ ($P < 0.0001$); home range $\chi^2 = 556.0$ ($P < 0.0001$); and core area $\chi^2 = 260.7$ ($P < 0.0001$).

Plant Community Type	Observed Proportion	Expected Proportion	Preference/ Avoidance
	Study Area		
Agriculture	0.05	0.23	–
PGC	0.07	0.21	–
AGC	0.13	0.27	–
Syal-Ronu-Rhgl	0.07	0.04	0
Crdo/Syal	0.19	0.05	+
Phma/Syal	0.07	0.05	0
Pipo-Psme/Hodi	0.25	0.11	+
Potr2/Syal-Prvi	0.04	0.02	0
Pipo/Crdod-Prvi	0.13	0.02	+
	Home Range		
Agriculture	0.03	0.26	–
PGC	0.07	0.14	–
AGC	0.13	0.30	–
Ronu-Syal-Rhgl	0.08	0.04	0
Crdo/Syal	0.19	0.06	+
Phma/Syal	0.07	0.05	0
Pipo-Psme/Hodi	0.26	0.08	+
Potr2/Syal-Prvi	0.04	0.04	0
Pipo/Crdo-Prvi	0.13	0.03	+
	Core Area		
Agriculture	0.04	0.20	–
PGC	0.06	0.11	–
AGC	0.13	0.29	–
Ronu-Syal-Rhgl	0.06	0.04	0
Crdo/Syal	0.20	0.06	+
Phma/Syal	0.08	0.05	0
Pipo-Psme/Hodi	0.24	0.12	+
Potr2/Syal-Prvi	0.05	0.07	0
Pipo/Crdo-Prvi	0.15	0.05	+

[1]'–' = avoidance, '+' = preference, and '0' = no selection.

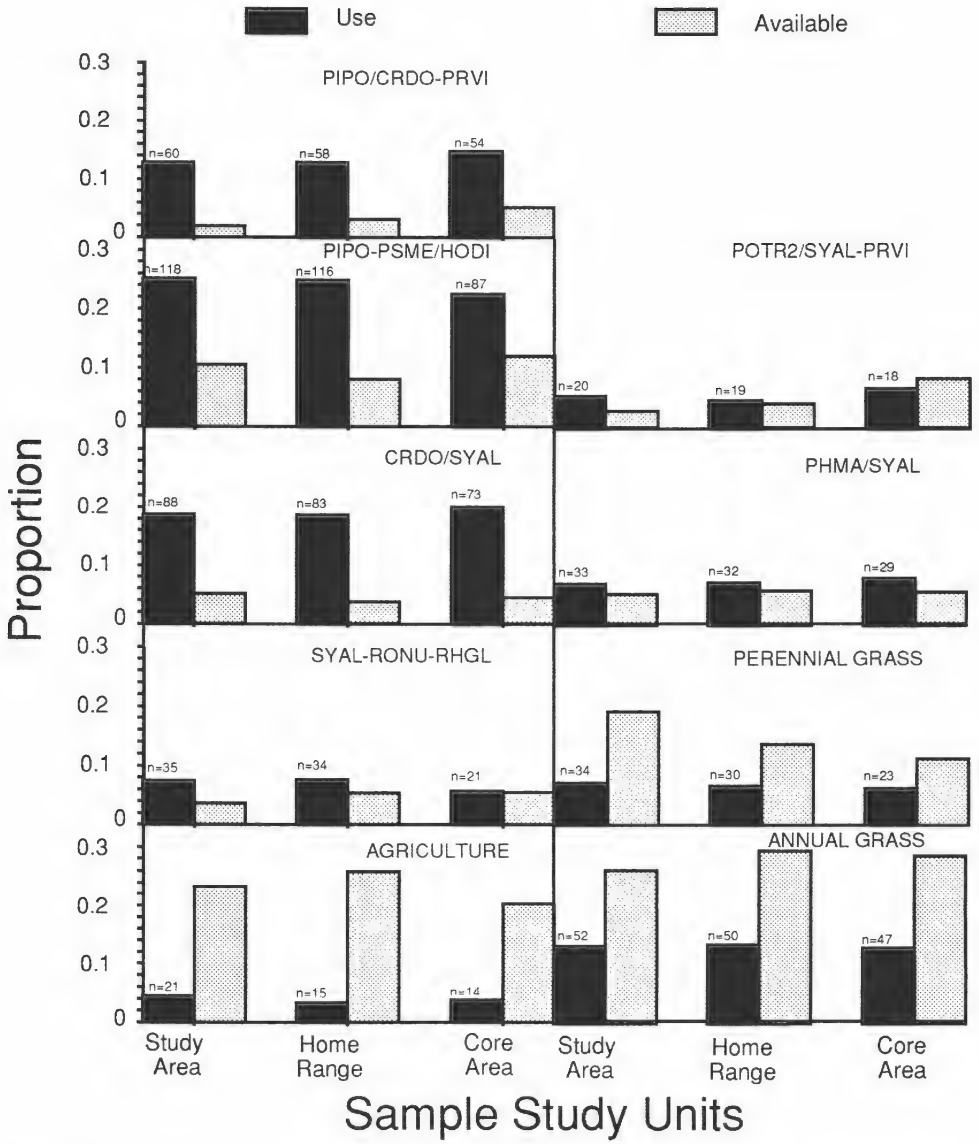

Figure 1. The proportion of use and availability of plant community types by white-tailed deer within 3 different sampling units during the winter 1985-86 along the Umatilla River, northeast Oregon. Sample sizes are 471, 447, and 366 for study area, home range, and core area, respectively. Plant community symbols are Syal-Ronu-Rhgl = *Symphoricarpos albus - Rosa nutkana - Rhus glabra*, Crdo/Syal = *Crataegus douglasii / Symphoricarpos albus*, Phma/Syal = *Physocarpus malvaceus / Symphoricarpos albus*, Pipo-Psme/Hodi = *Pinus ponderosa - Pseudotsuga menziesii / Holodiscus discolor*, Potr2/Syal-Prvi = *Populus trichocarpa / Symphoricarpos albus - Prunus virginianus*, Pipo/Crdo-Prvi = *Pinus ponderosa / Crataegus douglasii - Prunus virginianus*.

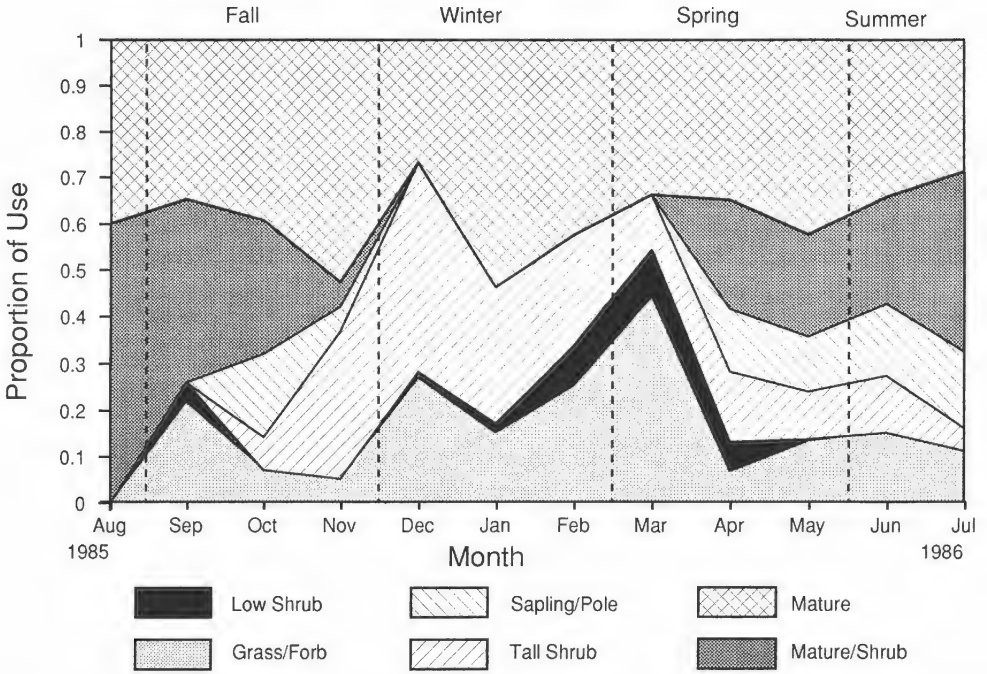

Figure 2. Cumulative proportion line graph of structural type use by white-tailed deer within the 95% harmonic mean home ranges during 1985-1986 (n = 937). Dotted vertical lines identify the 3 months within each season, labeled at the top of the graph.

Use of 4 winter structural classes was not homogeneous between deer (Table 3). Two deer used the tall shrub class in a greater proportion than all other classes, while use of the mature class was greater for the remaining 7 deer. Use was different from availability for all deer ($P < 0.0001$).

Deer use of structural classes in winter was different from availability when all locations were pooled within the SA, HM, and CA. Use of the grass/forb class was significantly less than availability in SA, HM, and CA. Use of the tall shrub class and mature class was greater than availability in SA, HM, and CA (Table 4).

Summer use relative to availability of structural classes was not homogeneous between deer ($P < 0.0001$) but was different from availability for each deer ($P < .02$) (Table 5). Grass/forb, tall shrub, and sapling/pole classes were not used by all deer, while mature/shrub and mature tree classes were used by all deer.

Summer use of structural classes was different than availability within home ranges and core areas ($P < 0.0001$) when locations were pooled (Table 6). Grass/forb use was less than availability. Use of sapling/pole and mature classes was greater than availability. Mature/shrub use was less than availability within the CA.

Topography

Slope, slope position, aspect, and elevation classes were all used different from availability ($P < 0.0001$) within the winter SA sample unit (Table 7).

The east aspect was used more than expected and 63 percent of this use occurred in tall shrub or mature types. The moister aspects including north, northwest, northeast, and east comprised 65 percent of all use. The south, southwest, and west aspects were used less than their availability. Most tall shrub use occurred on north, northwest, and northeast aspects.

Bottom slopes were used greater than expected, while the middle 1/3 and ridge slope positions were used less than expected. The lower 1/3 position received the greatest use but was not preferred.

TABLE 3. Heterogeneity chi-square test of use versus availability of structural types by individual white-tailed deer during the winter of 1985-86 within the Umatilla River drainage, northeast Oregon. Availabilities are based on the relative area of each structural type within the 95% harmonic mean home range. Expected values are listed directly below the observed values in parentheses. Overall $\chi^2 = 620.11$ ($P < 0.0001$, df = 24) and heterogeneity $\chi^2 = 156.96$ ($P < 0.0001$, df = 21).

Deer	Grass/Forb	Low Shrub	Tall Shrub	Mature Tree	Row χ^2	P (df = 3)
700	18	4	15	32	65.35	<0.0001
	(48.507)	(1.932)	(5.451)	(13.110)		
710	6	5	11	28	79.51	<0.0001
	(34.200)	(2.600)	(4.850)	(8.350)		
720	16	7	2	26	68.12	<0.0001
	(37.128)	(2.142)	(4.080)	(7.650)		
730	18	1	43	2	107.30	<0.0001
	(44.736)	(5.312)	(11.392)	(2.560)		
740	15	11	1	17	51.19	<0.0001
	(33.352)	(2.596)	(0.968)	(7.084)		
780	1	0	1	29	58.75	<0.0001
	(19.282)	(0.124)	(2.170)	(9.424)		
790	10	3	6	31	39.23	<0.0001
	(30.700)	(1.550)	(4.400)	(13.350)		
810	8	1	8	26	116.42	<0.0001
	(31.992)	(1.118)	(5.203)	(4.687)		
860	13	2	23	2	34.25	<0.0001
	(30.645)	(0.900)	(11.700)	(1.755)		

Eighty percent of the bottom slope use occurred in mature stands, while tall shrub and mature comprised 29 percent and 34 percent, respectively, of lower 1/3 use.

Use of the 11-30 percent and 31-50 percent slopes was greater than expected. The tall shrub and mature types dominated use within the 11-30 percent and 31-50 percent slope classes.

The lowest elevation class received almost half of the use. Almost half the use of the tall shrub and mature structural types, 49 percent and 53 percent, occurred in this class.

Distance to Hiding Cover

Distances to hiding cover ranged from 5 to 540 m (n = 139) with only 5 locations recorded further than 250 m. The relative cumulative frequency distribution for distance from hiding cover pooled into 10 m classes fitted the 2 parameter Weibull ($p > 0.95$, Fig. 3). The Weibull model predicts 50 percent, 75 percent, and 95 percent of use will occur within 44 m, 99 m, and 248 m of hiding cover, respectively.

Roads

Road densities within the HM home ranges were variable between types of road and between

TABLE 4. Goodness-of-fit chi-square test of use versus availability of structural types by white-tailed deer during the winter of 1985-86 within the Umatilla River drainage, northeast Oregon. Availabilities are based on the relative area of each habitat within the sample population study area, 95% harmonic mean home range, and core area. Simultaneous confidence intervals are based on a family alpha of 0.10. Study area $\chi^2 = 545.6$ ($P < 0.0001$), home range $\chi^2 = 439.4$ ($P < 0.0001$), and core area $\chi^2 = 252.6$ ($P < 0.0001$) (df = 3).

Structural Type	Observed Proportion	Expected Proportion	Preference/ Avoidance[1]
	Study Area (n = 471)		
Grass/Forb	0.25	0.71	–
Low Shrub	0.07	0.05	0
Tall Shrub	0.26	0.10	+
Mature Tree	0.42	0.14	+
	Home Range (n = 447)		
Grass/Forb	0.24	0.69	–
Low Shrub	0.08	0.04	0
Tall Shrub	0.25	0.10	+
Mature Tree	0.43	0.17	+
	Core Area (n = 366)		
Grass/Forb	0.23	0.62	–
Low Shrub	0.06	0.05	0
Tall Shrub	0.28	0.12	+
Mature Tree	0.43	0.22	+

[1] '–' = avoidance, '+' = preference, and '0' = no selection.

TABLE 5. Heterogeneity chi-square test of use versus availability of structural types by individual white-tailed deer during the summers of 1985-86 within the Umatilla River drainage, northeast Oregon. Availabilities are based on the relative area of each structural type within the 95% harmonic mean home range. Expected values are listed directly below the observed values in parentheses. Overall $\chi^2 = 1492.1$ ($P < 0.0001$, df = 28) and heterogeneity $\chi^2 = 1260.7$ ($P < 0.0001$, df = 24).

Deer	Grass/Forb	Tall Shrub	Sapling/Pole	Mature Shrub	Mature Tree	Row χ^2	P (df = 4)
700[1]	9	4	0	44	3	1133.7	<0.0001
	(48.43)	(7.80)	(1.37)	(1.50)	(0.90)		
700	20	10	0	3	2	39.9	<0.0001
	(30.10)	(3.26)	(0.70)	(0.49)	(0.32)		
710	0	0	1	13	27	55.7	<0.0001
	(4.67)	(0.25)	(4.06)	(23.86)	(8.16)		
720	3	0	30	7	5	24.5	<0.0001
	(3.27)	(0.37)	(16.15)	(22.08)	(4.14)		
730	1	1	30	4	8	14.9	<0.0043
	(4.00)	(0.86)	(19.78)	(12.90)	(5.46)		
780	0	4	24	8	7	29.8	<0.0001
	(2.37)	(1.72)	(15.27)	(21.50)	(2.15)		
790	1	3	0	9	27	87.1	<0.0001
	(26.00)	(1.68)	(1.60)	(2.60)	(8.04)		
810	0	6	1	7	31	45.5	<0.0001
	(1.85)	(3.96)	(1.35)	(25.20)	(12.69)		
860[1]	1	1	4	28	47	53.1	<0.0001
	(29.16)	(2.67)	(3.81)	(21.71)	(23.65)		
860	2	0	1	9	20	11.7	<0.0197
	(4.74)	(1.70)	(2.27)	(12.10)	(11.20)		

TABLE 6. Goodness-of-fit chi-square test of use versus availability of structural types by white-tailed deer during the summers of 1985-86 within the Umatilla River drainage, northeast Oregon. Availabilities are based on the relative area of each habitat within the 95% harmonic mean home range and core area. Simultaneous confidence intervals are based on a family alpha of 0.10. Study area $\chi^2 = 331.9$ and core area $\chi^2 = 280.6$ ($P < 0.0001$, df = 4).

Structural Type	Observed Proportion	Expected Proportion	Preference/ Avoidance[1]
	Home Range (n = 466)		
Grass/Forb	0.08	0.43	–
Tall Shrub	0.06	0.05	0
Sapling/Pole	0.20	0.14	+
Mature/Shrub	0.28	0.23	0
Mature	0.38	0.14	+
	Core Area (n = 321)		
Grass/Forb	0.05	0.36	–
Tall Shrub	0.04	0.06	0
Sapling/Pole	0.25	0.11	+
Mature/Shrub	0.22	0.30	–
Mature	0.43	0.17	+

[1] '–' = avoidance, '+' = preference, and '0' = no selection.

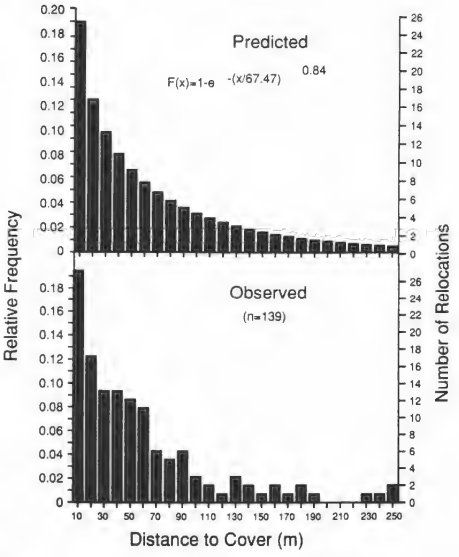

Figure 3. Predicted and observed probability distribution of white-tailed deer relocations as a function of the distance from hiding cover during the winter of 1985-86 in northeast Oregon. Predicted values are based on the fit of observed data to a 2 parameter Weibull distribution.

TABLE 7. Goodness-of-fit chi-square test of use versus availability of aspect, slope position, slope, and elevation by white-tailed deer during the winter of 1985-86 within the Umatilla River drainage, northeast Oregon. Simultaneous confidence intervals are based on a family alpha of 0.10. Availabilities are based on the relative area for each habitat within the sample population study area, inclusive of all winter home ranges. Aspect $\chi^2 = 131.7$ ($p < 0.0001$, df = 7; slope position $\chi^2 = 164.5$ ($p < 0.0001$, df = 4); slope $\chi^2 = 176.1$ ($p < 0.0001$, df = 3); and elevation $\chi^2 = 100.6$ ($p < 0.0001$, df = 3).

Class	Observed Proportion	Expected Proportion	Preference/ Avoidance[1]
	Aspect (n = 361)[2]		
North	0.15	0.11	0
Northeast	0.11	0.09	0
East	0.17	0.10	+
Ssoutheast	0.09	0.11	0
South	0.04	0.09	−
Southwest	0.04	0.10	−
West	0.18	0.24	−
Northwest	0.23	0.18	0
	Slope Position (n = 471)		
Ridge	0.05	0.16	−
Upper 1/3	0.21	0.24	0
Middle 1/3	0.17	0.24	−
Lower 1/3	0.30	0.24	0
Bottom	0.26	0.11	+
	Slope (n = 471)		
0-10%	0.24	0.25	0
11%-30%	0.36	0.24	+
31%-50%	0.35	0.21	+
>51%	0.05	0.30	−
	Elevation (n = 471)		
500m-610m	0.44	0.26	+
611m-730m	0.27	0.25	0
731m-850m	0.11	0.26	−
851m-975m	0.17	0.22	0

[1]'−' = avoidance, '+' = preference, and '0' = no selection
[2]Only locations with slope >10% were analyzed for use of aspect.

TABLE 8. Road densities (km/km²), year-round and seasonal, within white-tailed deer summer and winter 95% harmonic mean home ranges in northeast Oregon.

Deer	Main Roads		Seasonal Roads[1]	
	Summer	Winter	Summer	Winter
700	0.00	0.30	0.38	0.18
710	0.00	0.00	2.71	0.63
720	0.35	0.00	3.39	0.72
730	0.00	0.58	3.66	0.00
780	1.60	0.69	4.01	0.10
790	0.00	0.13	1.38	0.65
810	0.00	0.00	2.49	0.39
860	0.00	0.02	4.07	0.00
$\bar{\chi}$	0.24	0.22	2.76	0.33

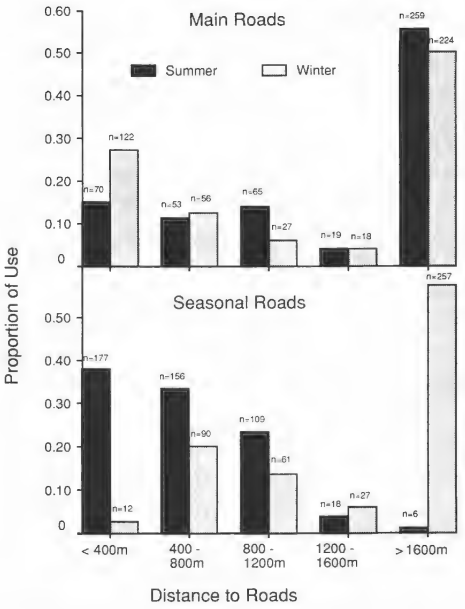

Figure 4. The proportion of use and distance (m) to main and seasonal roads within summer and winter home ranges of white-tailed deer in northeast Oregon from 1985-1986. Distances to roads have been grouped into 5 400-m classes with sample size displayed on top of each bar.

summer and winter (Table 8). Mean main road densities were 0.24 and 0.22 km/km² for summer and winter, respectively, and were not different ($T = -0.10$, $P = 0.54$). Seasonal road densities differed between summer and winter ($T = 2.52$, $P = 0.0006$) with mean densities of 2.76 and 0.33 km/km², respectively. Seasonal road densities were positively correlated to the amount of non-forested habitat within summer home ranges (Spearman's $r = -0.6848$, $p < 0.025$), although this relationship was not true for summer main road or either winter road densities.

Distance to roads exhibited similar results to road densities. The majority of use in both summer and winter occurred more than 1600 m from main roads while this only held true for seasonal roads in the winter (Fig. 4). Ninety-five percent of all summer use was located within 1200 m of seasonal roads.

Discussion

The method used for determining available habitat may affect conclusions on habitat selection (Johnson 1980, Porter and Church 1987). Tests of use and availability for all 3 winter sample units were very similar, both for plant communities and structural classes. The consistency between tests for both winter and summer suggested that all 3 methods for determining habitat availability were reasonable.

In winter white-tailed deer preferred mature forest structural types on moist sites with northerly aspects at low elevations which provided hiding cover due to the well-developed shrub understories. These findings were comparable to other studies in the northwest (Owens 1981, Keay and Peek 1980, Singer 1979, Mundinger 1981). Deer preferred tall shrub-dominated riparian zones, suggesting that in areas where conifer cover is scarce and winters are relatively mild, riparian shrub communities may be important to wintering deer.

All summer ranges contained an interspersion of plant communities and associated structural classes. All but one deer occupied sites dominated by ponderosa pine, Douglas fir, Engleman spruce, and grand fir, although no old-growth forests were found in or near the summer home ranges. The low shrub structural class was not found in measurable quantities within summer home ranges while sapling/pole and mature/shrub occurred in sizable quantities. The latter classes were generally the product of multiple-entry logging. Recent fires did not influence the majority of land occupied by white-tailed deer in the summer.

The variable use pattern by individuals suggests that vegetation structure was not an important environmental cue for summering white-tailed deer. Many studies on white-tailed deer have concluded deer select summer habitats based on the availability of preferred forage within or near cover (Kohn and Mooty 1971, Suring and Vohs 1979, Smith 1981, Murphy *et al.* 1985). Abundance and diversity of forbs in and near cover may also be important in determining summer habitat use in northeast Oregon.

Grass/forb communities were abundant and avoided in winter and summer, similar to other northwest studies (Keay and Peek 1980, Smith 1981). Deer using these communities were generally within relatively short distances of hiding cover. Kramer (1971) and Keay and Peek (1980) found use of open grassland habitats greater than expected in winter, when adjacent to suitable security cover. Agricultural lands provided the first new green forage available to deer in spring, and we observed heavy use of agricultural fields adjacent to hiding cover along the rim of steep canyons during early morning and late evening for a 1 to 2 week period prior to spring migrations.

The probability distribution developed for distance from hiding cover predicted use to increase almost exponentially as the distance decreases. The availability of the grass/forb and low shrub communities may be substantially overestimated given the relatively small area occupied by communities with value as hiding cover and the distribution of use away from hiding cover.

Summer main road densities averaging 0.24 km/km^2 reduced deer habitat effectiveness over 5 percent, while the mean seasonal road density of 2.76 km/km^2 reduced deer habitat effectiveness approximately 62 percent (Thomas 1979). Main road densities probably had little influence on summer home range locations. The relatively high seasonal road densities found in summer home ranges may be tolerated because of the high amount of hiding cover present.

Avoidance of main roads within winter home ranges was apparently due to the large amount of open habitat in the winter ranges. Avoidance of seasonal roads was not so obvious because they were closed in winter. Snowmobiles were generally used on existing roads and could affect white-tailed deer movements and area of use (Dorrance *et al.* 1975). All-terrain-vehicles were observed during early spring within the winter range. Nixon *et al.* (1988) found white-tailed deer use of forested tracts in Illinois was related to the amount of forest habitat in a refuge unavailable to hunting and off-road vehicles. In contrast, Drolet (1976) found white-tailed deer use greater along roads through clearcuts during May due possibly to reduced energy costs for travel, and lack of vehicle use at that time. Road densities in this study were probably not great enough to affect location of home ranges or use of habitats. More research would be required to establish the relationship of road densities to the use of winter and summer habitats.

Maintenance or increases in the amount of conifer cover along valley bottoms would benefit white-tailed deer. Patches of hawthorne in draws and adjacent to agricultural fields should be maintained.

Communities dominated by ninebark could be burned to improve forage values (Keay and Peek 1980) and as a precursor to other silvicultural practices which would promote their succession to conifers.

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Effects of Survey Frequency on Bird Density Estimates in the Shrub-Steppe Environment

Abstract

An assumption underlying the valid use of repeated line transect surveys is that the detectability of animals does not vary during the survey period. We conducted a line transect study of shrub-steppe birds to examine the relationship between the temporal sampling regime and the consistency of the resulting counts. Total counts of birds nesting in the sampled habitat were found to be significantly lower when sampling was repeated on a daily interval than on a weekly interval. Counts of birds not nesting in the habitat were unaffected by the sampling regime. We attribute this effect to changes in behavior of nesting birds in response to the repeated presence of the observer: western meadowlarks (*Sturnella neglecta*) were more likely to be silent and sage sparrows (*Amphispiza belli*) were probably temporarily leaving their territories when an observer reappeared on consecutive days. The temporal patterning of samples may therefore affect the mean and variability of density estimates using any of the available line-transect algorithms.

Introduction

Obtaining accurate density data is essential to studies dealing with wildlife demography and population change. Such data are often obtained by line transect counts, in which sightings of individuals are recorded whenever they are detected on or within a specified distance of a line of predetermined length. Line transect methods have long been used to estimate numbers of birds in terrestrial habitats (e.g., Merikallio 1951), and a great deal of attention has been given to improving estimates by modifying field methods (e.g., Emlen 1971) and analyses (e.g., Eberhardt 1978, Anderson *et al.* 1979).

The accuracy of density estimates derived from transect counts reflects the degree to which the assumptions of the method are met. The primary assumptions are: 1) individuals are randomly distributed within the sampled space; 2) the probabilities of observing an individual declines from unity immediately on the transect to zero at some distance at right angles to the transect; 3) no errors occur in measurement; 4) individuals are counted only once; 5) the behavior of individuals in one portion of the transect does not influence the detectability of individuals in other portions of the transect; 6) individuals are not likely to escape detection as a response to the observer; 7) detectability does not change during the sampling period; and 8) detectability does not vary with age or sex (Burnham *et al.* 1980, Franzreb 1981a).

A number of studies have examined the robustness of various transect methods to violations of underlying assumptions (e.g., Franzreb 1981a, Tilghman and Rusch 1981, Ekman 1981). The nonrandom distribution of individuals is generally recognized (Eberhardt 1978) and is countered by randomly locating transects within the sampling space. The nonconstant probability of detection versus distance from the transect is generally dealt with using any of several probability functions (e.g., Burnham *et al.* 1980) or correction factors (e.g., Emlen 1971). Similar correction factors are employed to correct counts for differences in detectability due to age or sex (e.g., Emlen 1977). Measurement errors are acknowledged but are less important with certain transect methods (Franzreb 1981a). Assumptions regarding behavior constancy of the individuals being sampled are dismissed less readily and often receive less scrutiny in study designs and analyses.

In 1986, one of us initiated a study of shrub-steppe birds using a line transect methodology. The purpose of this study was to evaluate habitat associations and time-trends in bird abundances and to assess statistical properties of the sampling regime itself. The present paper describes statistical properties related to the time interval between successive samples.

Methods

Study Area

The study area is located in the Cold Creek Valley on the U.S. Department of Energy's Hanford Site near Richland, Washington (Figure 1). The valley is composed of relatively undisturbed shrub-steppe

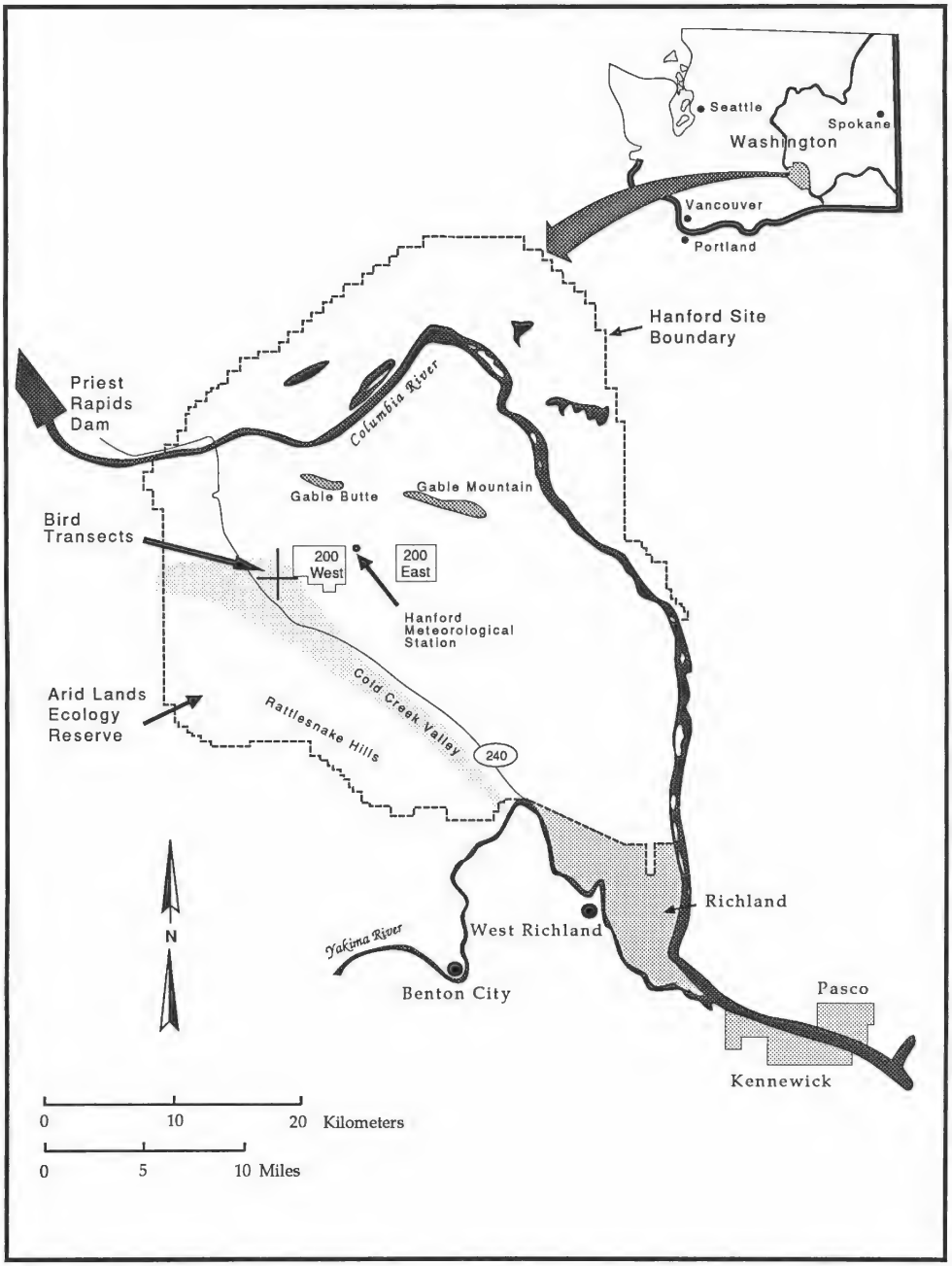

Figure 1. Location of study on the Hanford Site.

habitat dominated by annual and perennial grasses, especially cheatgrass (*Bromus tectorum*) and Sandberg's bluegrass (*Poa sandbergii*), with an overstory of widely spaced shrubs, including big sagebrush (*Artemisia tridentata*), spiny hopsage (*Grayia spinosa*), gray rabbitbrush (*Chrysothamnus nauseosus*), and green rabbitbrush (*C. viscidiflorus*).

Transect Surveys

Four line transects were established in 1986 along cardinal compass points. The lengths of the east and west transect were 1.69 km; the north and south transects were 2.66 km in length. Vegetation types traversed by the transects included big sagebrush/cheatgrass, spiny hopsage/Sandberg's bluegrass, and cheatgrass only (burned areas). Transect lines were marked with stakes at 0.1 km intervals within homogeneous habitat.

All transects were surveyed within 2 hrs of sunrise twice each week on consecutive days. These 24 hr surveys were repeated at approximately 1-week intervals for 30 weeks between 10 March and 2 October, 1987. Two observers performed the surveys simultaneously, with transects assigned to observers on a random basis each sampling day. On the first survey of the week, observations started first on randomly selected ends of each transect. On the subsequent day, the observers walked the halves of the transect in the reverse direction. In this fashion, observer identity was randomized over both transects and transects were sampled at equivalent times over the duration of the study period. Transects were walked at an approximate rate of 2.4 km/h.

The numbers, species, and distances from the transect of birds observed within 80 m of either side of the transect were recorded for each 0.1 km segment of each transect. Birds were identified to species using visual and aural cues. Bird behavior was recorded when the bird was first observed. Behavioral categories included Flyby (bird crossing the transect ahead of observer), Flush (bird flushing within 30 m of the observer), Sing (perched bird singing), and Perch (bird perched and silent). Categories were mutually exclusive, such that a singing bird was recorded under Sing and not also under another category, such as Perch; flushing birds that crossed the transect were recorded under Flush. Birds were not counted twice; the openness of the habitat and the habits of the birds allowed accurate tracking of individuals.

Data Reporting and Analysis

Data are reported as counts summed over all segments of both transects. Statistical analyses included time series analysis, Wilcoxon signed-ranks analysis, paired *t*-tests, and Chi-square tests for goodness-of-fit. Two-by-two contingency tables with fixed marginals (i.e., weeks versus sign of difference between counting periods) were analyzed using Fisher's exact test. Parametric analyses of counts were conducted on data transformed to square roots to normalize distributions. Two-tailed tests were applied in all cases of primary analysis, with a Type I error rate of 0.05 constituting a significant departure from the null. One-tailed tests were used where the null hypotheses included a direction.

Results

All Birds

Thirty-five bird species were observed during the transect walks (Table 1). Nine of these species nested in the shrub-steppe vegetation along the transects. The most frequently sighted birds were western meadowlarks and sage sparrows. European starlings were the most common species sighted that did not nest in shrub-steppe vegetation.

An average of 49.3 birds of all species were counted per survey during the study period when estimates from all surveys were included. However, when average counts were estimated using only the first of the consecutive surveys each week, the average for the survey period was 55.1 birds per survey. On a monthly basis, first-day counts were higher than mean counts based on two-day samples 7 months out of 8, the exception being March (Figure 2). Counts based on both sample sets showed similar trends over the study period, with peak numbers in April and a second peak in June. Counts declined from June to October for both sample sets.

During a period of declining population numbers, survey counts and resulting density estimates based on second-day surveys are expected to be lower than estimates based on first-day surveys throughout the decline phase. The average expected difference between the two estimates during any time period is the average daily rate of decline during that period (see Appendix A). For the present study, the differences in monthly bird counts between first-day and second-day samples

TABLE 1. Average number of birds counted on suveys from 10 March through 2 October 1987.[a]

Common Name	Scientific Name	Mean Count/ survey	Surveys when species detected
Shrub-steppe birds nesting along the transect			
western meadowlark[b]	*Sturnella neglecta*	12.04	60
sage sparrow	*Amphispiza belli*	5.44	51
burrowing owl	*Athene cunicularia*	1.32	44
horned lark	*Eremophila alpestris*	1.24	28
long-billed curlew	*Numenius americanus*	1.15	24
mourning dove	*Zenaida macroura*	0.75	24
loggerhead shrike	*Lanius ludovicianus*	0.75	22
lark sparrow	*Chondestes grammacus*	0.22	7
common nighthawk	*Chordeiles minor*	0.18	10
Other birds			
white-crowned sparrow	*Zonotrichia leucophrys*	5.03	6
European starling	*Sturnus vulgaris*	4.69	37
black-billed magpie	*Pica pica*	1.00	18
American robin	*Turdus migratorius*	0.51	9
barn swallow	*Hirundo rustica*	0.46	12
rock dove	*Columba livia*	0.39	4
common raven	*Corvus corax*	0.35	17
western kingbird	*Tyrannus verticalis*	0.35	13
brown-headed cowbird	*Molothrus ater*	0.19	8
savannah sparrow	*Passerculus sandwichensis*	0.13	3
American kestrel	*Falco sparverius*	0.08	6
Swainson's hawk	*Buteo swainsoni*	0.06	5
Townsend's solitaire	*Myadestes townsendi*	0.04	1
sage thrasher	*Oreoscoptes montanus*	0.04	3
northern flicker	*Colaptes auratus*	0.03	2
red-winged blackbird	*Agelaius phoeniceus*	0.03	2
Brewer's blackbird	*Euphagus cyanocephalus*	0.03	1
house finch	*Carpodacus mexicanus*	0.03	1
Brewer's sparrow	*Spizella breweri*	0.01	1
chipping sparrow	*Spizella passerina*	0.01	1
northern harrier	*Circus cyaneus*	0.01	1
northern oriole	*Icterus galbula*	0.01	1
red-tailed hawk	*Buteo jamaicensis*	0.01	1
rough-legged hawk	*Buteo lagopus*	0.01	1
Say's phoebe	*Sayornis saya*	0.01	1
vesper sparrow	*Pooecetes gramineus*	0.01	1

[a]Total number of surveys = 60.
[b]Species underlined were seen on at least 15% of surveys.

were much lower than the average rate of decline for all months when numbers were declining. The greatest rate of decline occurred between April and May, when numbers declined at a rate of 1.8 per day. However, monthly bird numbers based on second-day surveys during that period were lower than first day estimates by 29.9 ($\bar{x}_{day1}$ = 103.4, $\bar{x}_{day2}$ = 73.5).

The pattern of fluctuation in daily estimates departed significantly from random (runs test: z = 2.424, P = 0.0156). Counts fluctuated more frequently than expected based on a random model. Estimates were subjected to time series analysis to identify the strongest periodicity in the data. The greatest level of autocorrelation was for a lag of one (r = 0.429, SE = 0.129). The autocorrelation for lag of two was 0.289 (SE = 0.151). Autocorrelations for lags of greater time were all less than 0.135. Fourier transformation of the time series identified the primary cycle as the N_t to N_{t+1} signal, with the factor weighting over 7 times any other weighting.

The sample-to-sample differences identified in the time series analysis were examined further

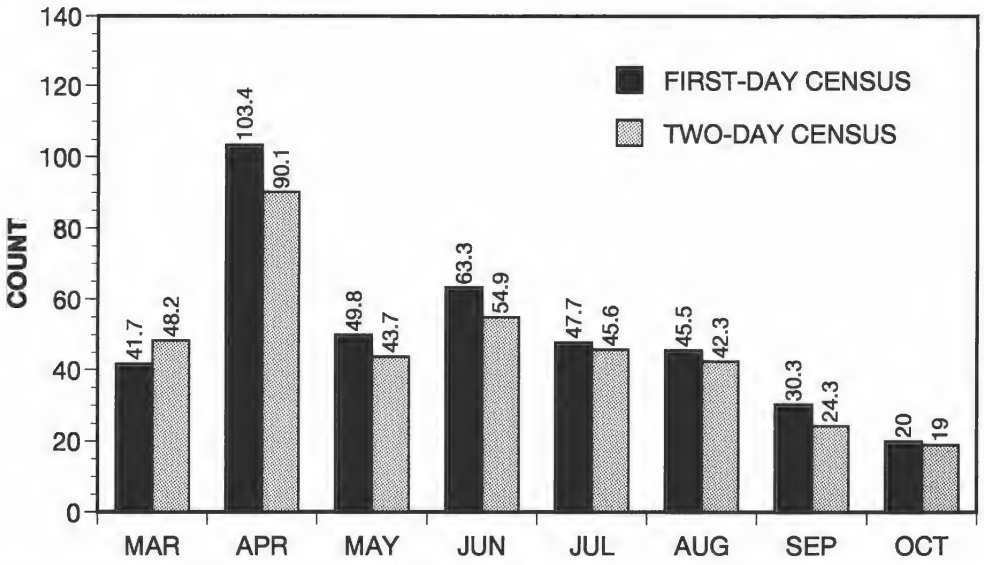

Figure 2. Average counts of all birds seen in the sampling transects based on weekly and twice-weekly samples.

using paired comparisons in a one-tailed test with the null hypothesis that second-day counts were no lower than the previous or subsequent estimates. The null hypothesis was rejected: Average counts on the second survey of the week were significantly lower than counts obtained the previous day (paired t-test: $t = 2.449$, $df = 29$, $P < 0.012$). Average counts were also lower on the second survey of the week than they were on the subsequent survey approximately six days later (paired t-test: $t = 1.751$, $df = 28$, $P = 0.045$).

The behavior of survey estimates was examined further by subdividing birds into two groups: those that nested in the shrub-steppe habitat along the transects and those that nested elsewhere, but which visited the area. Monthly estimates of nesting species exhibited a temporal pattern similar to the estimates for all birds, without the large peak in April (Figure 3). Estimates based on two samples per week were smaller than estimates based on the first sample each week for all months except March. In all cases when estimates were declining, the difference in estimates based on first-day versus second-day samples were greater than the average decline rate. Partial autocorrelations from the time series analysis showed the primary cycle to be between one sampling period and the next ($r = 0.255$, SE $= 0.129$). Fourier transformation weighted the first element over ten times that of any other. Runs test analysis, however, did not show a significant departure from random ($z = 0.758$, $P = 0.44$).

Survey counts of species that did not nest in the shrub-steppe habitat were less constant over time compared to the nesting species (Figure 4). Numbers of visiting species peaked dramatically in April, when large flocks of birds, probably migrants, made temporary appearances on the transects. Monthly estimates based on first-day samples were no larger, on average, than were estimates based on all samples. Paired comparisons showed no significant difference between first-day and second-day estimates ($t = 0.027$, $P = 0.978$). Autocorrelations were low for all time lags, although the greatest correlation was between one sample period and the next ($r = -0.208$, SE $= 0.153$). Fourier transformation weighting of the one-day lag was only twice that of the 2-period and 3-period lags. Thus the period-to-period cycle was much less strong for visitors than for birds nesting in the shrub-steppe habitat.

This difference was further explored using only those 14 species that were detected on at least 15% of the surveys (Table 1). Of these, 8 nested in the shrub-steppe and 6 were visitors. Counts for 7 of

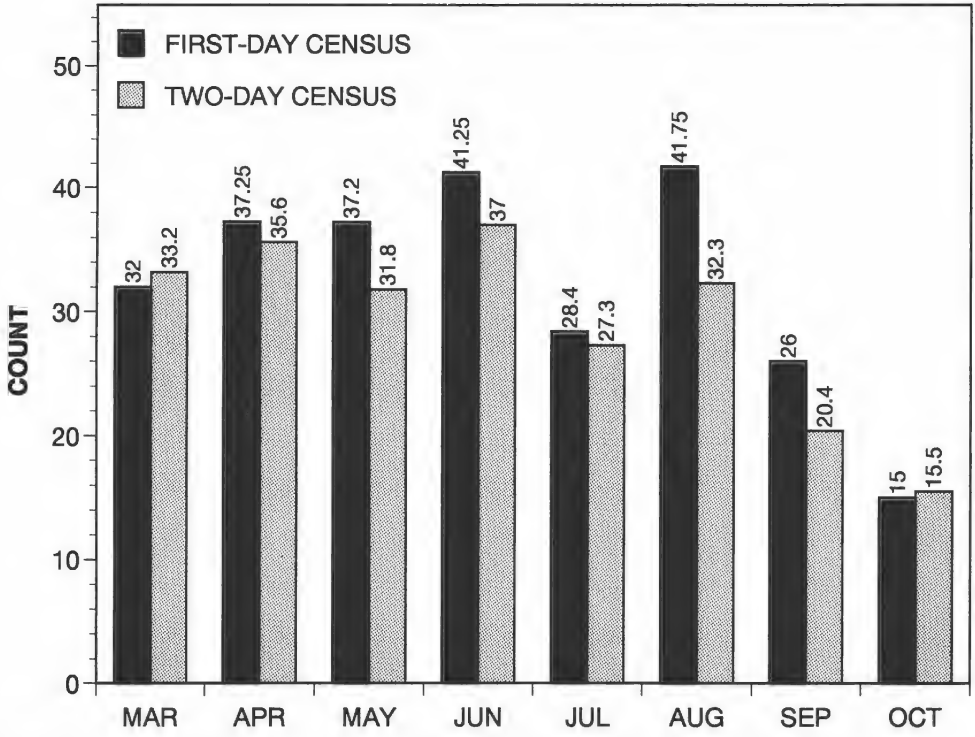

Figure 3. Average counts of birds nesting on the sampling transects based on weekly and twice-weekly samples.

the 8 species nesting in the shrub-steppe were greater on the first sample day than on the subsequent sample day for the entire study period (binomial $P = 0.035$). Only 2 of the 6 visitor species showed the same trend (binomial $P = 0.344$). The difference in counts for the 2 groups of species approaches significance (Fisher's Exact $P = 0.063$).

Western Meadowlarks

Western meadowlarks were the most abundant species on the transects, composing nearly one-third of all sightings. Average estimates of western meadowlarks on second-day samples (14.1 birds/survey) were significantly lower than counts on the previous day (18.1 birds/survey; paired-$t = 2.628$, $df = 29$, $P < 0.014$). One observation on day 200 (first-day sample) constituted a significant outlier that could not be normalized using standard transformations. Subsequent comparison using the nonparametric Wilcoxon signed-ranks test supported the conclusion made on the basis of parametric tests ($z = -2.408$, $P < 0.016$). Deletion of the outlier and its pair (day 201) from the parametric analysis did not affect the significance of the conclusion (paired-$t = 2.113$, $df = 27$, $P < 0.028$).

During the period from nesting to fledging (1 April to 30 June), counts were greater on the first survey of the week on 9 weeks, with the opposite occurring only on 2 weeks (binomial $P = 0.033$). During the flocking period after 30 June, first-day counts were greater than second-day counts during 8 weeks, with the opposite occurring on 5 weeks (binomial $P = 0.291$).

Counts of meadowlarks classed as singing and flyby during the entire study period were significantly smaller on the second day than on the first day of the week, although the likelihood that second-day counts would be lower than on the previous day was not significant (Table 2). Differences for other behavioral categories were not

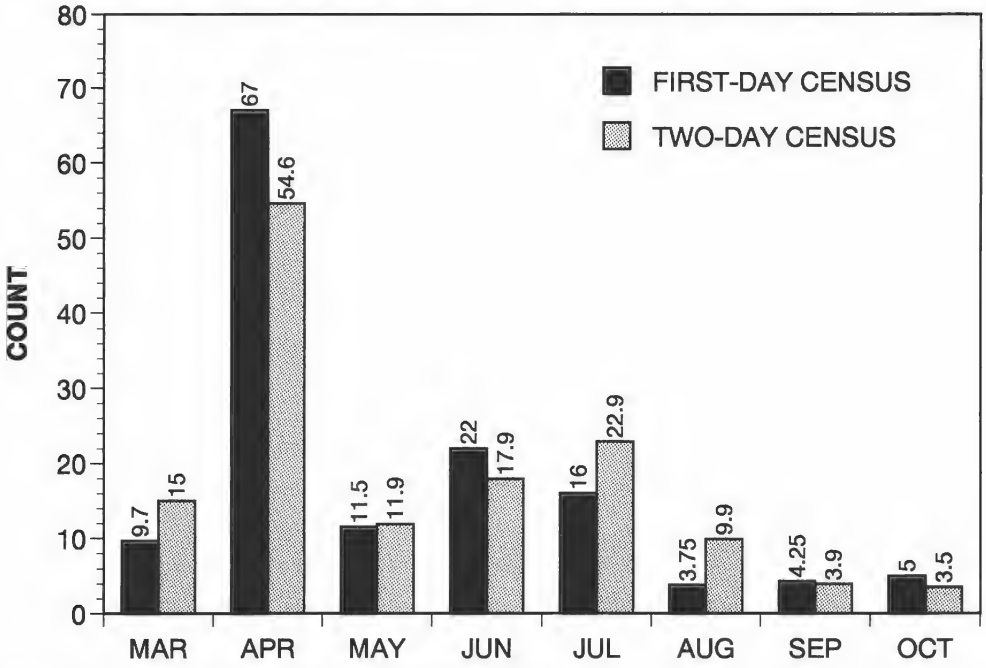

Figure 4. Average counts of birds visiting (not nesting on) the sampling transects based on weekly and twice-weekly samples.

TABLE 2. Analysis of western meadowlark counts according to activity at sighting.

	Sing	Perch	Flyby	Flush
Average First-Day	6.4	2.0	4.2	5.6
Average Second Day	5.3	2.2	1.9	4.6
Wilcoxon Z	−1.736	−0.436	−1.724	−0.555
One-tailed P	0.041	0.33	0.043	0.29
No. Day 1 > Day 2	15	12	17	14
No. Day 1 < Day 2	9	15	10	15
χ^2	1.500	0.926	1.815	0.034
P	>0.1	>0.1	>0.1	>0.5

significant. Counts of singing birds were lower on the second day than the first day during the nesting-to-fledging period on 9 weeks, with the opposite obtaining on 3 weeks (binomial $P = 0.073$). During the flocking period, no differences were observed for singing birds on first-day versus second-day samples on 5 weeks; first-day counts of singing birds were greater than second-day counts on 5 weeks, with the opposite occurring on 4 weeks (binomial $P = 0.5$). Comparisons for other behavioral categories did not depart significantly from random.

Sage Sparrows

Sage sparrows were detected during all but nine surveys and were the second most abundant bird on average. Counts of sage sparrows early in the study period were almost entirely of singing birds. After 9 July, no singing was heard, and subsequent counts were either of perching or flushing birds. No sage sparrows were counted after 4 September.

Counts of sage sparrows on the first survey of the week ($\bar{x} = 9.4$ birds/survey) were significantly greater than on the subsequent survey ($\bar{x} = 7.7$ birds/survey, paired-$t = 2.497$, $df = 24$, $P < 0.02$). Counts on first-day surveys were more frequently higher than counts on the following day but the difference was within the realm of sampling error (14 counts higher versus 8 counts lower, Binomial $P = 0.143$). No portion of the study period existed in which bird counts on any given pair of survey dates were more likely to show a common trend.

TABLE 3. Analysis of sage sparrow counts according to activity at sighting.

Statistic	Activity at Sighting			
	Sing	Perch	Flyby	Flush
$\bar{x}_{day\ 1}$	6.1	1.8	0.2	1.4
$\bar{x}_{day\ 2}$	5.6	1.2	0.2	0.7
Wilcoxon Z	−0.643	−0.679	−0.632	−1.512
One-tailed P	0.261	0.248	0.264	0.066
No. samples Day 1 count > Day 2 count	10	8	2	9
No. samples Day 1 count < Day 2 count	7	9	5	3
Binomial P	0.315	0.500	0.227	0.073

Analysis of counts according to the activity of the birds when first sighted shows no significant differences between paired survey dates for any activity (Table 3). Sage sparrows were rarely counted as flybys (8 of 48 surveys), so comparisons on this variable are not reliable. Counts of birds in other activity categories were lower on the second survey, though only the counts for flushing birds neared statistical significance. There was no significant tendency for trends from first-day to second-day samples to differ between nesting/incubation and flocking periods (Binomial $P > 0.3$).

Density Estimates

Density estimates are generally derived from line-transect survey data by applying a correction factor to observed counts (Burnham *et al.* 1980). This correction factor utilizes information on the distance from the transect to the observed individual to determine the expected number of individuals that are undetected, assuming that the probability of detection declines with distance from the transect according to some standard decay function (see Seber 1973, Burnham *et al.* 1980). Density estimates from consecutive surveys could therefore remain invariant despite differences in counts if average distances of sighted individuals from the transect increased on the second survey. This possibility was not upheld: no significant differences in average distance from the transect to the sighted individuals were found for shrub-nesting species as an aggregate or for any individual species (binomial $P > 0.5$).

Discussion

Selection of an appropriate sampling frequency for repeated transect surveys is crucial to obtaining accurate indices of density. Our analysis indicates that bird density indices derived from surveys repeated on a short-duration cycle can be significantly below estimates made from surveys on a longer duration cycle. In the present study, the average weekly bird count was consistently lower by more than 10 percent when surveys were taken on consecutive days rather than 1 week apart.

Differences in counts from first-day to second-day samples are expected when population numbers (or estimates of those numbers) are declining; however, the difference in estimates in the present study could not be explained by population decline alone. Remaining potential causes for the observed difference are limited to real differences in numbers or artificial differences resulting from bird behavior, observational conditions (e.g., poor weather on the second day), and/or sampling technique (e.g., the tendency for more-competent observers to sample on the first day of the week transects with higher bird densities). The only periodic aspect of the sampling design was that transects were walked in the reverse direction from one sample to the next. However, since starting points were chosen at random, it is highly unlikely that direction of travel would produce the trend observed. Weather conditions were random with respect to sample date, and timing of samples were constant with respect to sunrise.

Differences in bird numbers between first and second day samples were thus either a consequence of real differences or differences in detectability. In both cases, differences would be a function of observer-bird interaction. Real differences in numbers are unlikely unless the birds were more likely to leave the sampled area earlier in response to the approaching observer on the second survey than on the first survey. Most birds are

detected on transects by song alone (Cyr 1981). Thus differences in counts could also arise if normally singing birds were less likely to sing as a consequence of the repeated appearance of the observer. This change was noted for western meadowlarks during the nesting period.

In contrast to counts of meadowlarks, counts of singing sage sparrows showed no significant differences between first-day and second-day surveys. Counts of sage sparrows for all behavior categories were generally lower on the second day than on the previous day, although not significantly so, which is consistent either with the hypothesis that fewer sage sparrows were present on the second survey of the week, or the hypothesis that sage sparrows became less conspicuous on the second day by moving under cover.

There were no significant differences in counts between first-day and second-day surveys for species that visited the area of the transects but did not nest there. This is consistent with the suggestion that the difference detected for birds nesting in the shrub-steppe was a consequence of repeated bird-observer interaction on a short time frame. Visiting birds are less likely to be present in the same area day after day, in contrast to resident nesting birds.

Changes in behavior in response to repeated disturbance may be attributed either to habituation or conditioning. Habituation is the waning of response to a particular stimulus pattern presented repeatedly over sufficiently short intervals. Conditioning refers to the adoption of a particular behavior pattern as a result of associating a particular stimulus with a certain reinforcement. Habituated behavior patterns are readily restored by relatively short intervals without the stimulus. Conditioned responses are less readily extinguished (see Staddon (1983) for definitions and characteristics). Given that bird counts returned to higher levels within 5 days of the previous survey, habituation of resident birds to the observer rather than conditioning is likely to be the cause for lower counts. On daily surveys, nesting birds may cease to associate the observer with a potential predator or competitor. Consequently, birds may be less likely to exhibit warning displays (e.g., singing by western meadowlarks) or to stay on their territories (e.g., sage sparrows) during the second survey when the observer approached.

A few density estimation techniques explicitly take advantage of the alarm or territorial defense response of animals to human intrusions (e.g., territory mapping, Wiens 1969). Most techniques rely implicitly on behavioral patterns to allow infallible detection in at least some portion of the survey area (e.g., variable-strip and fixed width line transect methods, Emlen 1971, Burnham *et al.* 1980; variable circular-plot methods, Reynolds *et al.* 1980). Such complete detection regions serve as the basis for deriving either a spatial detection function or a "coefficient of detectability," which is then used to "correct" counts from portions of the sampling region where the probability of detection is assumed to be less than unity (e.g., Burnham *et al.* 1980). Even with such corrections, density estimates from transect or plot sampling schemes are consistently lower than estimates from spot mapping for all but the most conspicuous species (Franzreb 1981b, DeSante 1981, Tilghman and Rusch 1981). Habituation may further bias density estimates below true values.

An assumption essential to transect or plot-sampling techniques is that the detectability of the study population does not change during the sampling period (Seber 1973, Franzreb 1981a). Detectability varies with individuals (Diehl 1981), sexes (Mayfield 1981), and season (Ekman 1981), and various techniques have been proposed to correct for or minimize such variation. Less attention has been paid to the role of habituation as a source of error. As demonstrated in the present study, repeated sampling and resulting behavioral changes in birds can produce significant biases in counts of birds nesting on line transects. Subsequent estimates of bird density based on any of the available algorithms (see listing in Tilghman and Rusch 1981) will not only under-represent reality, but will be unstable because standard errors will depend on the mixture of sampling periodicities involved in the estimate. Standard errors will be smallest when habituation is low in all samples, and maximal when half the samples are affected by habituation and half are not. Standard errors will be low when habituation is common, but density estimates will be maximally biased. The birds nesting in shrub-steppe habitat in the present study exhibited behavioral changes when sampling periods were 24 hours apart. Shorter time intervals are likely to be even more effective at inducing such behavioral changes. Counts remained at high levels when sampling periods were at least 5 days apart; longer sampling intervals may lead to even higher counts per transect.

Habituation attenuates with time; it may also be abolished by altering the stimulus or its background (Hale and Almquist 1960). For example, an animal habituated to a noise may show renewed response when the noise is accompanied by a novel visual stimulus (Staddon 1983). It is, therefore, likely that habituation in transect sampling may be overcome by similar means. Determining these means presents some interesting experimental challenges.

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APPENDIX A

For any period undergoing linear decline in numbers, the expected count on day t is estimated by

$$N_t = N_0 - t\frac{dN}{dt} + e \qquad (1)$$

where N_t = number of individuals on day t,

N_0 -= number of individuals on day t = 0,

t = day since start of period,

$\frac{dN}{dt}$ = rate of change in numbers, and

e = random error.

Thus a series of w weekly samples would have an expected value during the sample period of:

$$\overline{N_1} = \frac{N_0 + (N_0 - 7\frac{dN}{dt}) + (N_0 - 14\frac{dN}{dt}) + \ldots + (N_0 - 7(w\text{-}1)\frac{dN}{dt} + we)}{w}$$

$$= N_0 - 3.5(w\text{-}1)\frac{dN}{dt} \qquad (2)$$

A comparable set of w weekly samples obtained the day after each of the previous samples would have an expected value of:

$$\overline{N_2} = \frac{(N_0 - \frac{dN}{dt}) + (N_0 - 8\frac{dN}{dt}) + (N_0 - 15\frac{dN}{dt}) + \ldots + (N_0 - (7(w\text{-}1)+1)\frac{dN}{dt})}{w}$$

$$= N_0 - 3.5(w\text{-}1)\frac{dN}{dt} + \frac{dN}{dt} \qquad (3)$$

Then, because the expected value of the difference between two random variables is the difference in their expected values,

$$\overline{N_1} - \overline{N_2} = (2) - (3) = \frac{dN}{dt} \qquad (4)$$

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The Status of Fish Populations and Management of High Mountain Lakes in the Western United States

Abstract

Fish stocking of mountain lakes in the western contiguous United States is a topic of increasing ecological concern and public debate. A synthesis of available information is needed to assess the diversity of stocking programs employed and their large-scale ecological implications. The purpose of this report is to provide an overview of the status of fish populations and management of high mountain lakes in the western U.S. based on interviews of state fishery managers in each of 43 regions in 11 states. The managers estimated that more than 95 percent of about 16,000 lakes were naturally fishless prior to stocking. Presently, about 60 percent of the total number of lakes and 95 percent of the deeper lakes (>3 m) and larger (>2 ha) lakes contain trout. Seventy-five percent of the lakes with fish are regularly stocked, including an estimated one-third that may have wild (self-sustaining) fish populations. Most regions manage mountain lakes fisheries with little survey or research data on which to base stocking programs. Few managers consider the health of indigenous trout populations, other aquatic species, lake ecosystems or the concerns of affected recreational users when conducting stocking programs. Intensive, on-going and largely indiscriminate stocking of lakes in most mountainous regions in the western U.S. may be causing large-scale degradation to aquatic ecosystems, indigenous fish, invertebrates, amphibian fauna and potential quality fisheries. Some management regions have expanded lake surveys and reduced stocking efforts to protect native and wild trout populations, quality fisheries, and pristine fishless lakes.

Introduction

Stocking fish in high mountain lakes has long been a source of concern and controversy (Hendee 1976). Although mountain lakes are typically small (<30 ha surface area) and remote, collectively they represent an important national resource, including most of the pristine aquatic systems and undamaged watersheds remaining in the country. Most recreation in National Parks, Wilderness and roadless areas centers on mountain lakes, although most research shows that only about half of the visitors to Wilderness high lakes actually fish (Hendee 1976). Controversy over high lake stocking has revolved around state fishery agencies and fishing groups concerned with maintaining and expanding fishery opportunities and Wilderness and National Park managers concerned with maintaining and restoring natural ecosystems (Nicola 1976, Pister 1977). Ecological concerns are increasingly supported by research findings. Recent studies in the Sierra Nevada, Rocky Mountains and North Cascades suggest that the ecological impacts of alien fish species on indigenous aquatic communities may indeed be severe, long lasting and widespread throughout the western U.S. (Reimers 1958, 1979; Bahls 1990a, 1990b, Liss and Larson 1991).

Since the late 1940's, the use of aircraft to stock trout in high mountain lakes has facilitated widespread and intensive introduction of non-native species throughout the mountain ranges of the western United States. However, the improvement in technology that has permitted fish introductions on a massive scale has far out-paced an understanding of the ecological consequences and basic knowledge of the types and extent of stocking programs conducted nation-wide. The potential for large-scale ecological impacts of stocked fish and the increased national concern for the protection and maintenance of biodiversity suggests that a high priority will need to be given to revising the goals and strategies of high lake management programs.

The purpose of this report is to provide an overview of the status of high mountain lakes in the contiguous western United States relative to fish populations and current fishery management methods and policies. The goal of the study is to provide a broader perspective of current management practices and their large-scale ecological implications in order to stimulate discussion and improvement of state and regional approaches to high lake fishery management.

Methodology

Study Area

The study area encompasses the mountainous regions of the contiguous western United States, comprising 43 state fisheries management regions in 11 states: Washington, Oregon, California, Idaho, Montana, Wyoming, Utah, Colorado, Nevada, Arizona and New Mexico. Lakes included

in this study represent specific regional or state definitions for what constitutes a "high" or "mountain" lake. In general, the lakes included in this study represent naturally formed lakes occurring above 800 meters in elevation.

Methods

Telephone interviews were conducted between 10 October and 25 November 1988 with the 43 regional fishery managers or biologists working for state fish and wildlife agencies in 11 states. In addition, district fishery managers within each region in Oregon and parts of California were interviewed. High lake research and management summary reports also were obtained from some regions. The interview consisted of a standard series of questions on the status of lake fisheries, type of survey methods employed, stocking criteria used, coordination with land management agencies, level of recreational use, type of angling regulations, ecological considerations given to stocking programs and current research activities.

Results and Discussion

Fishery status

About 16,000 high mountain lakes exist in the western contiguous United States (Table 1). However, the total numbers of lakes is approximate, since managers did not know the precise numbers of lakes, particularly fishless lakes, in their region. The largest concentrations of lakes are located in the Oregon and Washington Cascade Mountains, the Sierra Nevada Range of California and the Rocky Mountains of Idaho, Montana, Colorado, and Wyoming (Figure 1).

Mountain lakes in the western U.S. typically occur in glacial cirque basins and are ultra-oligotrophic owing to their occurrence at high elevations and within nutrient poor geological zones. Watersheds and lakeshore areas are highly sensitive to disturbance and exhibit slow recovery. Fisheries are characterized by low productivity owing to the cold, nutrient-poor waters and the short growing season.

About 40 percent of the lakes within the 11 western states are fishless (Table 1). Most of these fishless lakes are predominantly shallow (<3 m) and small (<2 ha) lakes which were either judged or proven to be incapable of supporting fish due to winter-kill or summer drought conditions. However, even many small, shallow lakes contain fish and are periodically stocked in Washington, Oregon, California, Colorado and Arizona. Most fishery managers estimated that less than five percent of the larger (>2 ha surface area), deeper (>3 m max. depth) lakes considered suitable as trout habitat remain in a pristine, fishless condition. The few areas where more than ten percent of the large lakes are maintained in a fishless condition include the National Parks, where stocking has been largely phased out, the remote Absaroka-Beartooth mountains in southwestern Montana and the state of Wyoming.

Fisheries managers estimated that probably less than five percent of the lakes contained fish populations prior to introductions of trout which began about 100 years ago. Most lakes remained fishless until the advent of aerial stocking and improved hatchery technologies in the 1940s. With passage of the Wilderness Act of 1964, stocking was limited by Federal guidelines to lakes that had been

TABLE 1. Approximate total number and percent of mountain lakes in each state within each fishery type.

	State											
Fishery Status	AZ	CA	CO	ID	MT	NV	NM	OR	UT	WA	WY	TOTAL
Total no. lakes	60	4131	1446	1791	1650	36	50	877	1080	2700	2000	15891
% lakes with fish	50	63	76	58	47	58	64	84	66	56	40	59
% lakes without fish	50	37	24	42	53	42	36	16	34	44	60	41
% large, fishless lakes	0	3	3	3	8	0	0	0	0	4	10	4
% lakes stocked	50	52	59	46	24	22	64	76	50	44	20	45
% unstocked wild trout lakes	0	11	17	13	24	36	0	8	16	11	20	14
% salmonid lakes	50	38	52	43	29	17	58	13	26	30	9	32
% brook trout lakes	0	21	20	12	17	42	6	70	38	22	21	23
% other fish lakes	0	4	4	3	1	0	0	1	2	4	10	4

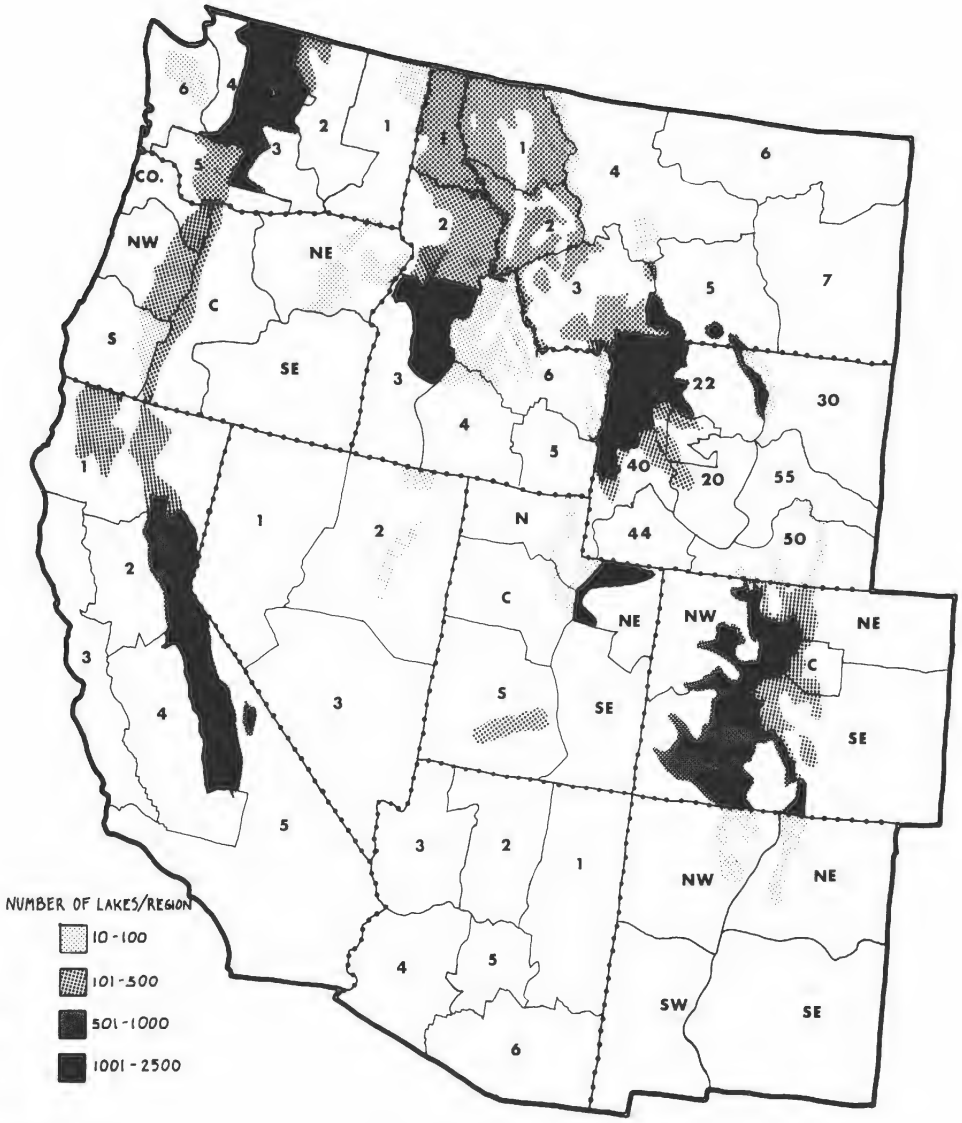

Figure 1. Number of lakes in mountainous areas of each state fishery management region in the western U.S.

stocked previous to Wilderness designation, providing at least some protection of naturally fishless lakes from state agency stocking programs (Figure 2).

The three primary fish species occurring in mountain lakes are rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarki*) and brook trout (*Salvelinus fontinalis*). Lesser numbers of golden trout (*O. aquabonita*), arctic grayling (*Thymallus arcticus*), lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), splake (brook-lake hybrid), rainbow-cutthroat hybrid, kokanee salmon (*O. nerka*), Atlantic salmon (*Salmo salar*) and several species of sucker, whitefish and minnow also occur. Although managers knew little about the

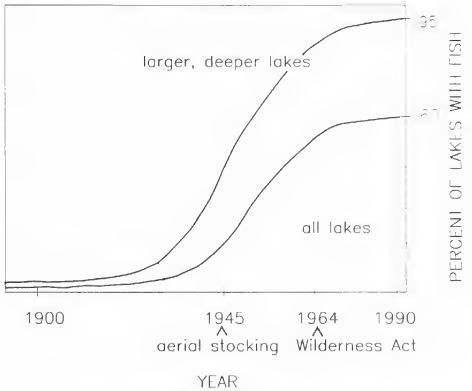

Figure 2. Hypothetical history of fish stocking for high mountain lakes in the western U.S. showing percentage of lakes containing fish for all lakes and larger (>2 ha surface area) and deeper (>3 m max. depth) lakes.

historical or current distribution of indigenous trout in lakes of most regions, they suggested that most lakes with indigenous trout have probably been subsequently stocked, leaving perhaps one percent of the lakes with relatively pure strains of native trout.

In most states, lakes originally planted with brook trout contain self-sustaining populations, usually with abundant numbers of small or stunted individuals. Notable exceptions include the Oregon Cascade mountains, where the majority of lakes continue to be stocked with brook trout every other year with few perceived over-population problems, and the highly productive lakes in the Boulder Mountain region of Utah which produce brook trout weighing 700 to 1000 grams within two years from the time of stocking.

Purpose of High Lake Fishery Programs

Regional managers stated that maximizing a diversity of fishery recreation opportunities (including "quality" fisheries) was the purpose of their high lake fishery program. Quality fisheries were generally defined as smaller populations of larger sized fish (>30 cm) supported within the carrying capacity of the lakes. Native and wild trout (self-sustaining by natural reproduction) populations are given high priority as "quality" fisheries in Colorado and Montana. Several regions, discussed later, have taken various steps to ensure that high lake stocking is consistent within the broader goal of protecting and enhancing indigenous trout, aquatic biodiversity and the ecological integrity of high lake regions.

Survey Methods

Most regions consider high lake management to be a low priority. Consequently, although stocking efforts are intensive and widespread, survey and research efforts have been minimal in most states (Table 2). Many lakes in the large wilderness and roadless areas of Montana and Idaho have never been surveyed, although they have been regularly stocked with fish for over 40 years. Most regions have an informal survey method of gill netting to obtain samples of fish for weight and length measurements. Some water quality samples and lake bathymetric measurements are taken as well. In some regions, fishery biologists and other personnel spend one to two weeks a year surveying lakes in an attempt to visit each lake in the region every five to ten years. Snorkeling instead of gill-net sampling is used by several districts in Oregon and California to estimate fish population and prey base characteristics of selected lakes.

The states of Wyoming, Colorado and Utah initiated long-term standardized fishery survey programs that included most of the mountain lakes in each state. In Colorado and Wyoming, most lakes were surveyed once to determine the status of the existing fish populations and the suitability for future stocking. Utah recently completed a second phase of surveys on about 600 lakes in the High Uinta Mountains in order to revise stocking rates established after the initial surveys, which were conducted 10-20 years ago. In the only systematic survey conducted in Montana, Pat Marcuson (1980) surveyed over 1000 lakes in the Absaroka-Beartooth region over a period of ten years.

More comprehensive limnological surveys have been conducted on 87 lakes in Colorado (Nelson 1988), 10 lakes in the Sierra Nevada (Reimers *et al.* 1955), 30 lakes in the Gospel Hump Wilderness (Espinosa 1976) and 189 lakes in the Nez Perce National Forest of Idaho (Bahls 1990a, 1987). Work in Washington includes surveys of 60 lakes on the Olympic Peninsula (Johnston 1973), 52 lakes in the North Cascades National Park (Liss and Larson 1991) and 30 lakes in Mt. Rainier National Park (G. L. Larson pers. comm., National Park Service, Oregon State University). In addition, Phase I of the Western Lakes Survey

TABLE 2. Percent of high lake fishery management regions in each state using various survey methods and management policies.

Survey methods and management policies	State											
No. of high lake mgt. regions	AZ 2	CA 4	CO 5	ID 5	MT 5	NV 2	NM 4	OR 5	UT 2	WA 6	WY 3	TOTAL %
Most lakes not surveyed	0	0	0	80	80	0	0	0	0	0	0	15
Infrequent fish status surveys	100	100	100	0	20	100	100	100	100	100	100	84
Comprehensive ecological surveys	0	0	0	20	0	0	0	0	0	34	0	5
Research studies	0	50	100	20	0	0	0	20	0	17	0	19
Active creel census program	0	25	40	40	0	0	0	40	0	83	0	21
No stock in native fish watershed	0	0	20	0	0	100	100	20	0	0	0	22
Stock only surveyed lakes	0	0	80	20	40	100	100	100	100	34	100	61
Stocking only with native strain	0	0	0	20	60	0	0	0	0	0	0	7
Stocking native and exotic strain	0	100	100	80	40	0	25	100	0	100	100	59
Stocking only exotic strain	100	0	0	0	0	100	75	0	100	0	0	34
Continued brook trout stocking	0	50	20	0	0	0	25	100	100	17	100	37
No supplemental stocking	100	25	0	80	60	0	50	0	0	17	0	30
No basis for stocking rates	0	25	0	80	60	0	0	0	0	0	0	15
Trial and error basis for rates	100	75	0	20	40	100	100	100	100	83	100	74
Quantitative index basis for rates	0	0	100	0	0	0	0	0	0	17	0	11
Stocking rotation period (years)	1	1-2	1-3	2-3	3-8	1-3	2-4	2	1-5	3-10	2-4	0
State-federal stocking plan	0	0	0	20	0	0	0	0	0	0	0	2
Concern with federal logging impact	0	25	0	60	0	0	0	60	50	17	0	14
Perceived recreation increase	100	100	100	100	100	100	0	100	100	100	100	91

was conducted in 1985 by the U.S. Environmental Protection Agency to determine the chemical status of 757 high mountain lakes considered to be at risk as a result of acidic deposition (EPA 1987).

A number of other methods have been used to obtain information on high lakes. Informal creel census, usually involving voluntary angler report cards available at the trail head, was used in many regions. Some states occasionally make use of state agency enforcement personnel to collect basic information (usually by angling) on the lake fishery. A few regions have cultivated high lake enthusiasts who give the state fishery agency information on the status of fish populations in high lakes that they visit. Washington has two user groups, the High Lakers and the Trail Blazers, which give stocking recommendations to the Department of Wildlife and, using backpacking methods, stock over 100 lakes a year.

Mountain lakes in the West have received little in-depth research compared with lowland aquatic systems (Goetze *et al.* 1989), but research activity seems to be on the increase. Current studies on high lakes include long term studies of the effects of fish stocking on the ecological communities of lakes in North Cascades National Park Service Complex, Washington (Liss and Larson 1991) and Wilderness Areas of the Nez Perce National Forest (Bahls 1990a). Nelson (1988) synthesized 20 years of research and survey data on high lakes in Colorado. Research has recently been completed on the population dynamics of stunted brook trout populations in response to density reduction in the Sierra Nevada mountains of California (Hall 1991). Work is in progress on developing a lake productivity index for use in estimating stocking rates in the northwestern Sierra Nevada (Morea pers. comm., California Department of Fish and Game).

Stocking Criteria

A. Lake habitat considerations

Few regions have active field investigations substantiating reasoning or results of stocking practices (Marcuson 1980). In terms of lakes considered suitable for stocking, most lakes in the West are assumed by managers to be able to support fish populations. Even many of the shallow, small lakes that provide marginal wintering habitat,

are stocked on a regular basis. Only one regional manager specifically stated that he would refrain from stocking a lake until it was surveyed. In Colorado and Wyoming, a small number of large, deep lakes at high elevations are not stocked due to their exceptionally low productivity. In addition, about 10 percent of the high lakes in Wyoming with suitable trout habitat are maintained in a pristine fishless condition.

B. Federal management considerations

Managers were aware of the "grandfather clause" of federal wilderness management guidelines that restrict stocking to lakes stocked previous to wilderness designation (USDA 1986). However, at least one region in Idaho continued to stock fishless lakes in wilderness areas until 1989. Considering that some managers assumed that most lakes have been stocked at one time or another, and the lack of state-federal planning coordination and limited survey data, rare fishless lakes are probably not adequately protected from stocking in some regions. However, the fishery management region encompassing the Absaroka-Beartooth Mountains of Montana maintains about 25 percent of 1000 lakes in a fishless condition as representative pristine lakes for baseline monitoring, research and wilderness values (Marcuson 1976).

National Park Service management policy adopted in 1977 (USNPS 1975) states in part that "The Service will. . . strive to maintain the natural abundance, behavior, diversity, and ecological integrity of native animals in natural portions of parks as part of the park ecosystem. . . No artificial stocking of fish species exotic to a park will occur; artificial stocking of fish may only be employed to reestablish native species. Naturally barren waters will not be stocked with either native or exotic fish species." However, sometimes heated controversies with the state fishery agency responsible for historical stocking of these lakes (Nicola 1976) have resulted in continuing stocking of a small percentage (< 10 percent) of lakes in most National Parks.

In a somewhat anomalous case, recent negotiations between the Washington Department of Wildlife and North Cascades National Park resulted in an agreement to continue stocking 50 percent of the lakes that would have reverted to a fishless condition with no stocking. In contrast, Rocky Mountain National Park allows no stocking of non-native trout species and initiated a native trout restoration program which has established self-sustaining native-strain greenback cutthroat and Colorado cutthroat in 11 lakes previously occupied by brook trout or other introduced trout (Rosenlund and Stevens 1988).

C. Fish species considerations

Several regions were taking steps to incorporate native trout protection and enhancement policies into their high lake management programs. New Mexico, Wyoming, and some regions of California have informal policies of not stocking lakes that drain into a stream system containing indigenous trout. Rocky Mountain National Park and a region encompassing the northeast Cascade mountains of Washington stock exclusively hatchery-reared trout originally indigenous to the region, while Colorado, Montana, Idaho, and New Mexico stock native-strain trout, while continuing to stock non-native trout species.

Most lakes in the West continue to be stocked with species, subspecies and stocks of trout not native to the watershed or region. Brook trout continue to be stocked in about 10 percent of the lakes stocked on a regular basis. However, most states have severely limited or discontinued brook trout stocking due to the observed tendency of the species to over-populate in most types of lakes. Brown trout and lake trout continue to be stocked occasionally to control over-populated brook trout lakes, although this method has met with mixed results and may actually compound the problem (Nelson 1988, Hall 1991).

D. Natural recruitment considerations

About 25 percent of the lakes containing fish in the West are not stocked owing to high levels of natural recruitment and self-sustaining fish populations (wild trout lakes). However, a variety of factors suggest that an additional 25 percent of the lakes with trout may not require further stocking to maintain fisheries. Most managers stated that stocking was conducted unless evidence of high natural recruitment was recorded for a lake. Given the lack of basic survey data in many regions and difficulty of identifying low to moderate levels of natural recruitment in the fish populations which are periodically stocked, the potential for unnecessary stocking is great. Also, intensive surveys of lakes in the Nez Perce National Forest indicated that 50 percent of the 130 lakes stocked on a regular

basis were probably capable of maintaining self-sustaining fisheries (Bahls 1990a). Likewise, National Park Service policy changes in the late 1960s which resulted in severe limitations on stocking, left self-sustaining trout populations in about 25 percent of the lakes previously stocked in national parks in California and Colorado (Wallis 1976, Rosenlund and Stevens 1988). The smaller percentage of wild trout lakes in the Parks may be due to the exceptionally marginal, high elevation spawning habitat and high angling pressure in these areas.

Only a few regions in Washington and Montana have a policy of not stocking lakes with any recognized natural recruitment. Montana, with a strong emphasis on maintaining wild and native fish populations in stream and river systems, appears to be the strongest supporter for maintaining wild trout populations in mountain lakes, shifting the burden of proof to permit stocking of only those lakes where it is clearly necessary to maintain fish populations. Supplemental stocking "when in doubt" is seen as an unnecessary risk to personnel involved in aerial stocking operations, a waste of management resources and potential cause of damage to quality wild trout fisheries and wilderness values (Marcuson 1976).

While most regions use supplemental stocking or an increase in stocking rates and frequencies to adjust to various levels of recruitment and angling pressure, several regions have adopted more restrictive angling regulations or are considering the implementation of such regulations to reduce the harvest and maintain a "quality" or wild trout fishery. In Rocky Mountain National Park, depletion of self-sustaining native-strain trout populations is prevented by a two fish per day bag limit. The Absaroka-Beartooth region of Montana has proposed a three fish limit. Colorado has long debated the idea of imposing slot limits, where trout within a specified size range would be released unharmed (Nelson 1988). On the other hand, in Colorado, Montana and Idaho, angling regulations allow the take of additional brook trout. According to Nelson (1988), the liberal regulation probably has little effect on reducing the abundant numbers of small and stunted fish that occur in most lakes containing this species, but probably does little harm either.

Stocking Rates and Frequencies

Most regions claim to manage high lakes by the "seat of the pants" method, presumably meaning in part that stocking rates and frequencies are based on limited or intuitive knowledge of the lakes in the absence of standardized or quantitative method for deriving appropriate stocking rates. Trial and error was the phrase most often heard, suggesting that stocking rates are based on past results in terms of the desired size, condition and relative abundance of fish. However, the past results upon which stocking rates are based varies considerably between regions. Montana and Idaho have relatively little data on which to estimate appropriate stocking rates, whereas in the Oregon Cascades, with fewer lakes per regional manager, higher fishing pressure and easier access to the lakes, there seems to have been more opportunity to evaluate stocking rates and make the necessary corrections.

Regions of Colorado rely primarily upon a stocking rate index based on research and surveys conducted by Nelson (1988) over a period of 20 years. The index incorporates lake elevation and estimated angling pressure (low, moderate, high) to derive appropriate annual stocking rates. For lakes in the Olympic Mountains of Washington, Johnston (1973) derived stocking rates from an "environmental parameter index" based on lake elevation, water alkalinity and food sources (shrimp and zooplankton) and other factors. Many regions, including those in Colorado, Utah, Washington and Wyoming, claim to have decreased stocking rates substantially since the 1940's and 1950's in response to lake surveys which indicated that existing stocking levels were resulting in populations of stunted and small fish.

Most regions stock at 62 to 620 fish/ha (25 to 250 fish/acre), depending upon the status of the existing fish population, perceived productivity and angling pressure at a lake. The frequency of stocking varies from one to eight years. Oregon plants mostly brook trout every other year and would stock every year if funding allowed. Most states stock fry or fingerlings on a set frequency of every two to five years for all lakes in the area, although some regions vary the frequency from two to eight years for specific lakes, depending on the perceived level of use, level of productivity and occurrence of other lakes in the area.

In the Absaroka-Beartooth region of Montana and the northeastern Cascades of Washington, the time period between fish plantings is between five to eight years and stocking cycles are staggered within a drainage basin (Marcuson 1980). The reasons given for such management are to:

1) provide a diversity of fishing opportunities—from abundant, small trout to lesser numbers of large, "trophy" trout in a lake over time and also between lakes in a drainage basin; 2) disperse recreational use among the lakes by varying the fishing opportunity available in a particular lake (from no fish present to trophy fish present) over time; 3) allow prey populations to replenish low productivity lakes during the period that trout populations are at a low level or not present in the lake; 4) increase the survival and growth rates of stocked fry due to lower predation associated with fewer large fish remaining in the lake and more abundant food resources available; 5) improve the cost-effectiveness of the stocking program by less frequent stocking and use of expensive helicopter time; and 6) lessen the impact of fish stocking on the lake ecosystem and associated wilderness values.

Stocking Methods

Use of fixed wing aircraft and helicopters are the major methods currently used to stock mountain lakes in the West. Backpacking and horse-packing trout fry into a lake are used rarely. In the Absaroka-Beartooth region, horse or backpacking methods are sometimes substituted for aerial stocking in the vicinity of a lake of special concern, such as a lake containing a pure stock of golden trout or native trout, to reduce the risk of stocking the lake accidentally while stocking lakes in the area (Marcuson 1980).

State and Federal Management Interactions

About 80 percent of the mountain lakes in the West are located in National Forests managed by the U.S. Forest Service, 15 percent in National Parks managed by the U.S. National Park Service and the remaining lakes fall under a variety of federal, state or private ownership. Most high lakes in the National Forests are located in designated Wilderness Areas, with the remainder mostly in roadless areas.

Management interaction between the federal and state agencies in regards to mountain lakes is limited, usually consisting of an annual notification from the state to the federal agency concerning the lakes to be stocked in that year. Few state fishery regions have formal "memorandums of understanding" listing the trout species or lakes which can and cannot continue to be stocked, although Federal Wilderness Management Guidelines recommend such action (USDA 1986). Based on baseline survey data collected and analyzed between 1986-1990, Nez Perce National Forest and the fishery management region of north-central Idaho are in the process of preparing a cooperative stocking plan for lakes in this National Forest. With the recent emphasis of the Forest Service on fishery programs, it seems likely that the cooperative funding and coordination between fishery and land management agencies to address mountain lake survey and management needs will increase.

In some regions, a major point of contention between state fishery and federal land managers is the building of new logging roads that increase accessibility to lakes and result in greatly increasing fishing pressure. Managers stated that the quality of the fishing experience is impaired by increased lakeshore impacts related to heavy recreational use and nearby logging operations and clear-cuts. Also, with increased fishing pressure on these relatively low productivity waters, fishery managers have not been able to sustain a "quality" trout fishery of large fish, but have switched to a "put and take" fishery of small catchable fish stocked more frequently into the lakes.

Recreational Use

Just as basic information is lacking on the fisheries resources of mountain lakes in most areas of the western United States, so too is an understanding of the people for whom stocking is conducted. No fishery region had conducted studies on the values or desires specific to high lake anglers or wilderness users. Managers' most commonly stated goals of providing a diversity of fishing opportunities and quality fisheries (in terms of larger fish in greater abundance) may have little relationship to the public's broader conception of a quality backcountry or wilderness experience.

Most regional managers perceived an increase in the recreational use of high lakes in recent years, with associated impacts on lakeshore vegetation and fish populations. The Sierra Nevada Mountains of California appear most heavily impacted, with most regions reporting a level of use far above that which fragile lakeshore areas can sustain. Fisheries consisting mainly of stunted and dense brook trout populations seem to be little affected by increased fishing pressure (Hall 1991). Staggering the stocking of lakes in a watershed, as discussed

above, is a standard method of trying to disperse use among a larger number of lakes, although only a few regions also use a lengthened time between stockings.

Long-term suspension of stocking at over-used lakes has been a matter of much debate (Cordone 1977, Wallis 1977, Nicola 1978). In some regions of Washington and California, suspension of stocking is considered a legitimate tool to disperse recreational users from heavily used areas. However, some regional fishery managers in Colorado are resisting requests by the Forest Service to discontinue stocking of over-used lakes, maintaining that use should be controlled by the land management agency through a special permit system, rather than indirectly, through a suspension of fish stocking.

Rather than discontinuing stocking to reduce impacts, Wyoming was seeking federal approval to stock additional pristine fishless lakes in Wilderness Areas as means to disperse use, but dropped the proposal due to ecological concerns and lack of U.S. Forest Service support. In general, most of the sociological research suggests that increasing fish stocking as a means of reducing recreational impacts may be counter-productive. Studies of backcountry users in many areas reveal that fishing is a relatively minor part of their overall visit. Manipulating the fishery would probably have a relatively small impact on the incentive of visitors to go to different places (Hendee 1976). Secondly, a highly curvilinear relationship exists between human use and impact, with relatively low levels of use producing high levels of impact and slow recovery in high elevation areas. Thus, a program to redistribute use would probably result in an increase in aggregate resource impact, ironically increasing the stress on high mountain fisheries and other values rather than reducing it (Stankey pers. comm., Oregon State University).

In Rocky Mountain National Park, pack animal use is restricted to areas below timberline and main trails. A permit system restricts camping to designated areas located at least .5 to 1 km from most lakes. The restrictions appear to keep lakeshore and fishery impacts at an acceptably low level, despite very high use of the Park overall (B. Rosenlund pers. comm. Fish and Wildlife Service).

Research Natural Areas

About 20 lakes in the western contiguous United States are designated as Research Natural Areas (RNA) under the U.S. Forest Service system. The majority of lakes with the RNA designation are located in the National Forests of Idaho, due largely to the efforts of Dr. Fred Rabe and others at the University of Idaho. Lakes proposed for RNA classification are usually managed as representative pristine ecosystems, with no fish stocking, road building or timber harvest permitted in the lake basin. Most regional fishery managers surveyed seemed amenable to the possibility of RNA designation of selected lakes in their regions for reasons of habitat protection and baseline study and monitoring, provided that a curtailment of fish stocking did not have significant impacts on fishery recreation.

Conclusion

Management of high lakes in the western contiguous United States can perhaps best be summarized as intensive, on-going and largely indiscriminate stocking of lakes in most mountainous areas. Most regions stock mountain lakes with non-native trout species and with limited or nonexistent survey data upon which to make basic stocking decisions, such as the identification of wild trout lakes (self-sustaining) that do not require further stocking. Most regions appear to have little concern for protection of native fish species in lakes or downstream systems, no evident concern for maintaining representative pristine lakes, and no consideration of the effects of trout stocking on indigenous fauna, aquatic ecosystems, and lakeshore recreational impacts. Furthermore, most regions appear to manage fisheries with little understanding of the high lake anglers whom they serve.

With virtually all mountain ranges in the contiguous western United States affected by more than 40 years of largely indiscriminate stocking practices, large-scale ecological disturbances and loss of biodiversity appear to be real possibilities. The elimination of many indigenous aquatic invertebrates following brook trout introduction to a lake in the Sierra Nevada was well documented by Reimers (1958, 1979). Recent research on 189 lakes of Nez Perce National Forest in Idaho (Bahls, 1990a and b) and 60 lakes in the North Cascades (Liss and Larson 1991) indicate significant differences in the biotic communities of lakes with and without fish, probably caused by fish predation on vulnerable invertebrates and amphibians. Degradation of potential quality fisheries throughout the

West by wasteful and unnecessary stocking also seems likely.

In the single-purpose drive of a fishery manager to make maximum use of fish stocking technology for the alleged purpose of providing for a small minority of the public that fish in remote mountain lakes, one might draw an analogy to the forest manager who strives to make as much timber available for harvest as soon as possible, irrespective of the losses to other resources or users. If fishery managers are to adequately serve the public as a whole, "optimum sustainable yield" must take the place of "maximum sustainable yield."

As Phil Pister (1977), regional fishery manager for the California Department of Fish and Game stated, "My obligation to provide and perpetuate a diverse and undisturbed invertebrate fauna is as great as it is to provide a creel full of trout; possibly greater, in that biological integrity dictates that I should give preference to endemic fauna. It is extremely important that we set aside a significant portion of the lake resource in as undisturbed a state as possible to provide for the generally unpredictable needs of future generations whose views and philosophies are likely to be completely different from our own."

Reform of high lake fish stocking programs to improve the condition of fisheries and wilderness ecosystems is largely the responsibility of regional fishery managers in each state. Reform necessitates shifting the burden of proof from favoring quantity fisheries to quality fisheries and ecosystem integrity, two compatible goals. As Aldo Leopold states in *A Sand County Almanac* (1966), "A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong otherwise." A revised program would ensure that stocking would cease in lakes with no survey data or having the potential to maintain a self-sustaining fishery. Fishless lakes would not be stocked due to their rarity and value as representative pristine systems for long term scientific monitoring and research, maintaining biological diversity and protecting a prey base reservoir for colonizing lakes depleted by fish. The specific management recommendations that follow are based on management practices and policies currently in use by some fishery management regions in the West.

1) Increase lake survey efforts and discontinue stocking of unsurveyed lakes. Design surveys to obtain fishery and ecological data necessary for: a) long term biotic, human use and environmental monitoring, b) classification of lakes for fishery management purposes into four classes (I. Fishless, II. Self-sustaining [wild and native trout], III. Stockable [suitable and unsuitable habitat subclasses], and IV. Further study [questionable natural reproduction with re-survey after 8-10 year hold on stocking]).

2) Develop cooperative funding and support between state fishery agencies and the U.S. Forest Service for high lake survey work and management plans.

3) Stock only the species of trout indigenous to the drainage basin. Obtain native brood stock from sources as close to the actual lake drainage as possible.

4) Identify watersheds with native trout populations and cease stocking of any lakes located upstream.

5) Lengthen the number of years between stockings to 4-8 years and stagger stocking years within a watershed.

6) Check available lake survey data to identify lakes with naturally reproducing fish populations and suspend stocking in these lakes. Eight to ten years from the last stocking conduct a simple fish survey to determine if the fishery is sustainable without stocking.

7) The rarity of lakes with suitable fish habitat (>2 ha surface area and >3 m max. depth) which remain in a pristine condition in the West makes it imperative that no further stocking of "new" or currently fishless waters occur. As a guideline for management of wilderness lakes, at least 50% of the total number of lakes in the management region or Wilderness Area should remain fishless, including at least 10% of the larger, deeper lakes potentially suitable for a fishery. Consider discontinuing stocking in selected representative lakes to meet this objective.

8) Limit stocking to a list of lakes developed in coordination with the land management agency. Cease irregular stocking of beaver ponds and shallow lakes.

9) Encourage Research Natural Area designation to provide long-term protection of representative pristine lakes and watersheds on National Forest land, particularly areas with no protection by Wilderness designation.

10) Implement restricted bag limits or slot limits on an area-wide basis to maintain quality fisheries in lakes with low natural reproduction or high angling pressure, rather than using more frequent stocking or supplemental stocking of wild populations.

11) Experiment with not stocking over-used lakes to determine if it is an effective means of dispersing use.

12) Educate the public and involve them in high lake survey and planning efforts.

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Incidence of Wound-Associated Infection by *Cytospora* sp. in Mountain Alder, Red-Osier Dogwood, and Black Hawthorn in Oregon

Abstract

Wildlife biologists are concerned that mortality of mountain alder (*Alnus incana*), a dominant riparian species in Oregon and Washington, would alter wildlife habitat. We chose to determine the cause of the mortality in alder and also examine the absence of dieback of associated species of red-osier dogwood (*Cornus stolonifera*) and black hawthorn (*Crataegus douglasii*). One hundred and fifty living stems each of alder, dogwood, and hawthorn were subjected to pathogenicity tests with the fungus *Cytospora* sp., the suspected pathogen. Trees of each species were wounded to the phloem or the xylem or left unwounded and then inoculated with *Cytospora* sp. After two growing seasons, incidence of infection was significantly higher in alder than in dogwood or hawthorn. Significantly more infection occurred in wounded alder stems than in unwounded stems. Cambial electrical resistance for alder was significantly higher (1) for inoculated than for uninoculated wounds and (2) for xylem wounds than for either phloem wounds or unwounded stems. We conclude that *Cytospora* sp. is associated with stem cankering and mortality of mountain alder in northeastern Oregon. This is the first report of mountain alder as a host for *Cytospora* sp. in Oregon. Because associated tree and shrub species are not affected, alder dieback should not seriously affect fish or wildlife habitat.

Introduction

Mountain alder (*Alnus incana* (L.) Moench) is a dominant plant species along watercourses in Oregon and Washington, where it provides shade and helps to maintain cool water temperatures critical for anadromous and other valuable fish species. Alder also provides cover for wildlife dependent on riparian zones (Thomas *et al.* 1979). In recent years, much of the alder has been dying, whereas associated shrub species such as black hawthorn (*Crataegus douglasii* Lindl.) and red-osier dogwood (*Cornus stolonifera* Michx.) do not seem to be affected. Wildlife biologists are concerned that alder mortality will alter wildlife habitat.

Diseased trees exhibit multiple branch cankers and branch mortality. A fungus tentatively identified as *Cytospora* sp. was consistently isolated from canker margins (Filip *et al.* 1989). Shaw (1973) reported only one species of *Cytospora* on alder in the Pacific Northwest: *C. pulcherrima* Dearness & Hansbrough in British Columbia, where the fungus was found fruiting on fire-damaged stems of *A. tenuifolia* Nutt. (=*A. incana*) (Dearness and Hansbrough 1934). The objective of our study was to further characterize the relationship between fungus and host by testing two hypotheses: (1) alder is highly susceptible to infection by *Cytospora* sp., but black hawthorn and red-osier dogwood are resistant, and (2) stem wounding is required for infection.

Methods

The research site was a 4-ha area in the Grande Ronde River drainage, Wallowa-Whitman National Forest, Oregon. All selected trees were free of cankers or other injuries. Variability from multiple wounds, wound aspect, and wound height above ground was reduced by making only one wound per stem on the north side at 1.4 m above ground. Stem diameters at 1.4 m ranged from 3 to 5 cm. Stems were numbered at the groundline with a metal tag. All treatments were applied in spring (April 1986), the probable time of maximum natural spore release and infection.

One hundred and fifty living stems each of alder, hawthorn, and dogwood were subjected to six treatments (25 stems/treatment). These treatments, randomly assigned to each stem, were (1) wounded (xylem) and inoculated, (2) wounded (phloem) and inoculated, (3) unwounded and inoculated, (4) wounded (xylem) but uninoculated, (5) wounded (phloem) but uninoculated, and (6) unwounded and uninoculated. Only 444 of 450 total stems were actually sampled because six stems could not be relocated after two growing seasons.

Cultures of *Cytospora* sp. were obtained from cankers on infected alders near the study area.

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Bark was removed from cankers, and wood chips (5 x 5 x 15mm) were removed from necrotic wood and placed onto potato dextrose agar. The genus *Cytospora* was identified based on colony morphology and color (Spielman 1985). Only one isolate was used for all inoculations.

Wounds (314 mm^2) were made with a 2-cm-diameter cork borer sterilized each time with 50 percent ethanol. Stems were surface-sterilized with ethanol before wounding. Phloem wounds penetrated only the inner bark; xylem wounds penetrated the cambium into the xylem. Bark disks were removed and replaced with a 2-cm-diameter agar plug (mycelium side toward pith) from 30-day-old cultures on potato dextrose agar. The agar disk was held in place with a wrap of Parafilm™. Wounded but uninoculated stems received a sterile agar plug. Unwounded but inoculated stems were marked in pen, and agar containing mycelium was placed on the marked but uninjured bark and held in place with a Parafilm™ wrap. Unwounded and uninoculated stems received a sterile agar plug.

In May 1987, cambial electrical resistance (CER) was measured (nearest K ohm) with a Shigometer Model OZ-67 (Osmose Wood Preserving Co., Buffalo, NY). The needle probes, sterilized with 50 percent ethanol, were pushed into the wood 1 cm above and below each treatment site.

In July 1987, after two growing seasons, the condition of the foliage on treated stems was observed for symptoms of advanced infection (chlorosis, stunting, death). The stem diameter at 1.4 m above ground was recorded again. A 1-m section of stem containing the treatment site was removed, placed in a plastic bag with the metal tag, returned to the laboratory, refrigerated, dissected, and cultured within 48 hours.

In the laboratory, the current wound area was calculated by measuring two diameters (nearest mm) at the longest and widest points between new callus tissue or living bark tissue. These diameters were multiplied together and then multiplied by 0.75 to approximate the area of an ellipse. The maximum length and width of discolored wood was measured (nearest mm) after the bark was aseptically removed. The discolored area was calculated the same way as the wound area.

Isolations were made from each stem. Ten wood chips (5 x 5 x 15 mm) were removed aseptically with a wood gouge at 2-cm intervals vertically and horizontally from each treatment site. Tissue type (healthy or discolored) was recorded for each wood chip. Five chips were sequentially plated onto potato dextrose agar. Cultures were maintained for 4 weeks at room temperature. The genus *Cytospora* was identified on the basis of colony morphology and color (Spielman 1985). No attempts were made to identify other fungal species.

Significant ($P \leq 0.05$) differences in isolation frequency among treatments were tested with chi-square analysis through the CATMOD program in the SAS/STAT Package Version 6 (SAS Institute Inc. 1987). Continuous response variables were analyzed by using the Advanced Statistics SPSS/PC+ (Norusis 1986). Discolored area, wound area, cambial electrical resistance, and percentage of change in stem diameter [(final diam.-initial diam.)/initial diam.] x 100 were subjected to a 2 x 3 x 3 factorial analysis of variance. Percentages were analyzed with arc sine transformation. When significant differences were found, means were subjected to Fisher's least significant difference test.

Results

Isolation Frequency

Cytospora sp. was consistently isolated from within discolored wood surrounding the original wound and from the margins of discolored and clear tissue in alder (Figure 1). A significantly higher isolation frequency of *Cytospora* sp. was obtained from alder than from dogwood or hawthorn (Table 1). Both inoculated and uninoculated stems of alder became infected, whereas only inoculated stems of dogwood and hawthorn became infected—but at very low frequencies. No infection occurred in unwounded alder treatments. There was no significant difference in the amount of infection between inoculated and uninoculated stems: some natural infection of alder occurred in wounded but uninoculated treatments. Many of the Parafilm™ wraps around each wound deteriorated by the end of the first growing season, and most were gone by the end of the second growing season. Except for two stems of dogwood, no unwounded stems became infected. There was no significant difference in isolation frequency between xylem wounds and phloem wounds.

After two growing seasons, none of the inoculated trees displayed foliage symptoms (chlorosis, stunting, death). Only 5 of 444 sample trees died

Figure 1. Among artificially wounded and inoculated alder stems, those affected have sunken areas (left) with discolored tissue (arrow) beneath the bark (right).

TABLE 1. Frequency of stem infection by *Cytospora* sp. in 444 artificially inoculated and uninoculated stems after two growing seasons.

		Number of stems*		
			Wounded	
Species	Treatment	Unwounded	To phloem	To xylem
Alder	Inoculated	0(0)a	16(64)b	12(50)b
	Uninoculated	0(0)a	5(22)b	6(26)b
Dogwood	Inoculated	2(7)a	2(8)a	3(12)a
	Uninoculated	0(0)a	0(0)a	0(0)a
Hawthorn	Inoculated	0(0)a	1(4)a	0(0)a
	Uninoculated	0(0)a	0(0)a	0(0)a

*Number in parentheses is percentage of total stems with *Cytospora* sp. Within a column or row, frequencies followed by the same letter are not significantly ($P \leq 0.05$) different according to chi-square analysis by the CATMOD procedure.

after two growing seasons. Two of these were dogwoods: one wounded and inoculated and the other unwounded and inoculated. Two were hawthorns: one wounded and inoculated and the other wounded and uninoculated. The one dead alder was unwounded and inoculated. *Cytospora* sp. could not be isolated from the treatment area of any of the dead trees. In all five cases, the trees apparently died from causes other than *Cytospora* sp.

Wound Size

After two growing seasons, phloem wounds were significantly larger than xylem wounds for all species (Table 2). Wounds inoculated with *Cytospora* sp. were not statistically different in size than uninoculated wounds. Except for dogwood xylem wounds, all inoculated wounds were larger after two growing seasons than they were originally. Xylem wounds that were uninoculated were all smaller after 2 years than they were originally, but phloem wounds that were uninoculated were the same size as or larger than the original wound.

TABLE 2. Wound size after two growing seasons in 294 stems artificially wounded and either uninoculated or inoculated with *Cytospora* sp. Wounds were originally 314 mm^2.

		Wound area (mm^2)*	
		Wound depth	
Species	Treatment	Phloem	Xylem
Alder	Inoculated	1232a	496b
	Uninoculated	313a	134b
Dogwood	Inoculated	343a	77b
	Uninoculated	458a	82b
Hawthorn	Inoculated	696a	339b
	Uninoculated	440a	95b

*Within a column or row, means followed by the same letter are not significantly ($P \leq 0.05$) different according to Fisher's least significant difference test.

Wound-Associated Discoloration

As stated above, *Cytospora* sp. was consistently isolated from discolored tissue surrounding wounded alder stems. None of the wounds had discoloration that completely girdled the stem. There were no statistically significant differences in amount of discoloration between xylem wounds and phloem wounds and between inoculated wounds and uninoculated wounds (Table 3). It is obvious from isolation results (Table 1) that the wound-associated discoloration in dogwood and hawthorn, both inoculated and uninoculated, was caused by microorganisms other than *Cytospora* sp.

Stem Diameter Growth

Within each tree species, diameter growth after two growing seasons was not significantly different (1) between stems with inoculated or uninoculated wounds or (2) between wounded or unwounded

TABLE 3. Wound-associated discoloration after two growing seasons in 294 stems artificially wounded and either uninoculated or inoculated with *Cytospora* sp.

		Discolored area (mm^2)*	
		Wound depth	
Species	Treatment	Phloem	Xylem
Alder	Inoculated	1447a	1538a
	Uninoculated	334a	214a
Dogwood	Inoculated	478a	1737a
	Uninoculated	603a	1320a
Hawthorn	Inoculated	922a	1338a
	Uninoculated	676a	1350a

*Within a column or row, means followed by the same letter are not significantly ($P \leq 0.05$) different according to Fisher's least significant difference test.

TABLE 4. Increase in diameter of 444 stems either uninoculated or artificially inoculated with *Cytospora* sp., after two growing seasons.

		Diameter increase (%)*		
			Wounded	
Species	Treatment	Unwounded	To phloem	To xylem
Alder	Inoculated	18c	28d	22d
	Uninoculated	20c	29d	27d
Dogwood	Inoculated	10a	6a	11a
	Uninoculated	9a	7a	9a
Hawthorn	Inoculated	14ab	11b	11ab
	Uninoculated	8ab	16b	13ab

*Within a column or row, means followed by the same letter are not significantly ($P \leq 0.05$) different according to Fisher's least significant difference test.

TABLE 5. Cambial electrical resistance (CER) 1 cm above and below a wound or corresponding location in 444 stems artificially inoculated or uninoculated with *Cytospora* sp., after two growing seasons.

		CER (K ohms)*		
			Wounded	
Species	Treatment	Unwounded	To phloem	To xylem
Alder	Inoculated	28ab	34b	59c
	Uninoculated	27ab	26ab	28b
Dogwood	Inoculated	20a	23ab	20a
	Uninoculated	20a	20a	21ab
Hawthorn	Inoculated	29b	32b	34b
	Uninoculated	29b	30b	29b

*Within a column or row, means followed by the same letter are not significantly ($P \leq 0.05$) different according to Fisher's least significant difference test.

stems—except for alder, which grew more when wounded ($P = 0.028$, Table 4). Alder grew significantly ($P < 0.01$) more in diameter than either dogwood or hawthorn.

Cambial Electrical Resistance

Cambial electrical resistance above and below a wound was significantly ($P < 0.01$) different among species (Table 5). Higher CER values usually indicate reduced host vigor. The highest CER occurred around xylem wounds of inoculated alder. Such wounds had significantly ($P < 0.01$) higher CER than uninoculated wounds or unwounded stems. There was no apparent correlation between CER and either wound size or amount of wound-associated discoloration.

Discussion

The fungus associated with the alder dieback has been identified as *Cytospora* sp., an anomorph of several species of *Valsa* (L. J. Spielman, pers. comm. 1990; Filip and Parks 1991). Species of *Valsa* are separated by disk color, ostiole arrangement, and ascospore size and therefore require the teleomorphic fruiting bodies that occur only on natural cankers in the field. We were not able to obtain these. Nevertheless, no species of *Valsa* has been reported on alder in Oregon (Spielman 1985). It is quite possible that the fungus in question is *C. chrysosperma* (Pers.: Fr.) Fr. (=*C. pulcherrima*), which is the anomorph of *V. sordida* (Spielman 1985) and was reported as *C. pulcherrima* on mountain alder in British Columbia (Dearness and Hansbrough 1934).

We suspect that *Cytospora* sp. may be causing the damage observed on alder in northeastern Oregon, although our study did not prove this—for two reasons: (1) canker development, stem girdling, and foliar symptom expression may take longer than the 2 years we allowed and (2) natural infection of uninoculated wounds made unclear the role of the fungus in canker development.

Empirical and experimental data indicate that stem wounding is required for fungal infection. Stem wounding in northeastern Oregon can occur in several ways: the most common is from damage by domestic cattle, deer, or elk that frequently use riparian zones containing alder (Thomas *et al.* 1979). Mass movement of river ice also causes periodic killing and wounding of trees and shrubs in riparian zones (Filip *et al.* 1989). Wounding does

not have to be so severe that the xylem is exposed: wounds to the inner bark are severe enough to result in infection. It is rare that an entire clump of alder is killed; only wounded stems are affected, and sprouting is common below killed branches. We could not determine the time between infection and stem dieback because in all cases infected stems were destroyed for sampling before the development of advanced symptoms.

Although we have observed alder dieback in other riparian zones in eastern Oregon besides the Grande Ronde River basin, the geographical extent of alder dieback in Oregon or other parts of western North America has not been determined. We did not determine whether other species of Pacific Northwest alder (*A. sinuata* (Regel.) Rybd., *A. rubra* Nutt., and *A. rhombifolia* Nutt.) are affected by *Cytospora* sp. Wildlife managers need not be concerned that alder dieback will seriously affect fish or wildlife habitat. Associated tree and shrub species, such as dogwood and hawthorn, are not affected.

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Gray Whale Feeding in a Northern California Estuary

Abstract

During the summer of 1989 a gray whale, *Eschrichtius robustus,* was discovered feeding in the Klamath River estuary of northern California. Distinct feeding behavior and feeding excavations were observed. Prey items were determined using SCUBA and hand-held core samplers. The tube-dwelling amphipod *Corophium spinicorne* was found in dense aggregations. The whale appeared to concentrate its feeding where amphipods were most dense. These findings suggest that gray whales feed selectively on benthic infauna during the summer months as far south as northern California.

Introduction

Gray whales, *Eschrichtius robustus,* migrate along the coast of California to and from their primary summer feeding grounds in the Bering and southern Chukchi Seas (Rice and Wolman 1971). In these arctic feeding areas the gray whale's major prey item is the benthic tube-dwelling amphipod *Ampelisca macrocephala* (Nerini 1984). Gray whales are known to summer along the coasts of British Columbia, Washington, Oregon, and California (Dohl *et al.* 1981, Darling 1984, Nerini 1984) and apparent feeding behavior has been observed. However, most of these reports have not documented prey items or feeding on benthic infauna (animals which inhabit bottom sediments) in areas south of Vancouver Island, British Columbia (Dohl *et al.* 1981, Oliver *et al.* 1984, Kim and Oliver 1989).

During the summer of 1989, we observed two gray whales in the mouth of the Klamath River estuary in northwestern California. This study describes the feeding activities of one of these whales and documents bottom substratum and prey.

Study Area and Methods

The Klamath River estuary is partially bounded on the west by a sand spit and on the northeast by a high-relief shoreline partly strewn with large boulders which provide several excellent vantage points from which to observe the whales (Figure 1).

Behavioral data are based on observations, of an approximately eight-meter-long juvenile, made during July and August 1989. Local residents reported occasional sightings of a second, larger, gray whale for two days in July; however, we did not confirm the presence of another whale until September. We observed and photographed the smaller whale from the bluffs, the sand spit, and by kayak. Its distinctive dorsal and rostral markings made it individually recognizable. We recorded its general behavior, movement patterns, dive times, surface intervals, and the number of blows per surfacing (Wursig *et al.* 1986). General behavior was categorized as feeding, traveling, resting, or other. Feeding was defined as repeated dives in specific areas, the whale often rolling on its side, and surfacing while trailing sediment plumes from its mouth (Nerini 1984).

On 27 July a free-diving survey of the estuary, consisting of four transects (Figure 1), revealed that the top layer of bottom sediment was composed of a dense aggregation, or mat, of tube-dwelling amphipods. This mat was bisected in the middle by a somewhat poorly defined natural channel. During the survey we photographed and recorded the presence and appearance of the amphipod tube mat, other organisms, substratum type and water depth. On 8 August marker buoys and SCUBA were also utilized to investigate the bottom in specific areas where the whale was observed to be concentrating feeding effort.

In two areas of the estuary we used SCUBA to collect random core samples penetrating the bottom sediment to a depth of three centimeters below the bottom layer of the amphipod tubes (Figure 1). The first group of four cores ("channel samples"; 0.0050 square meters each) was obtained between the estuary channel and sand spit. The

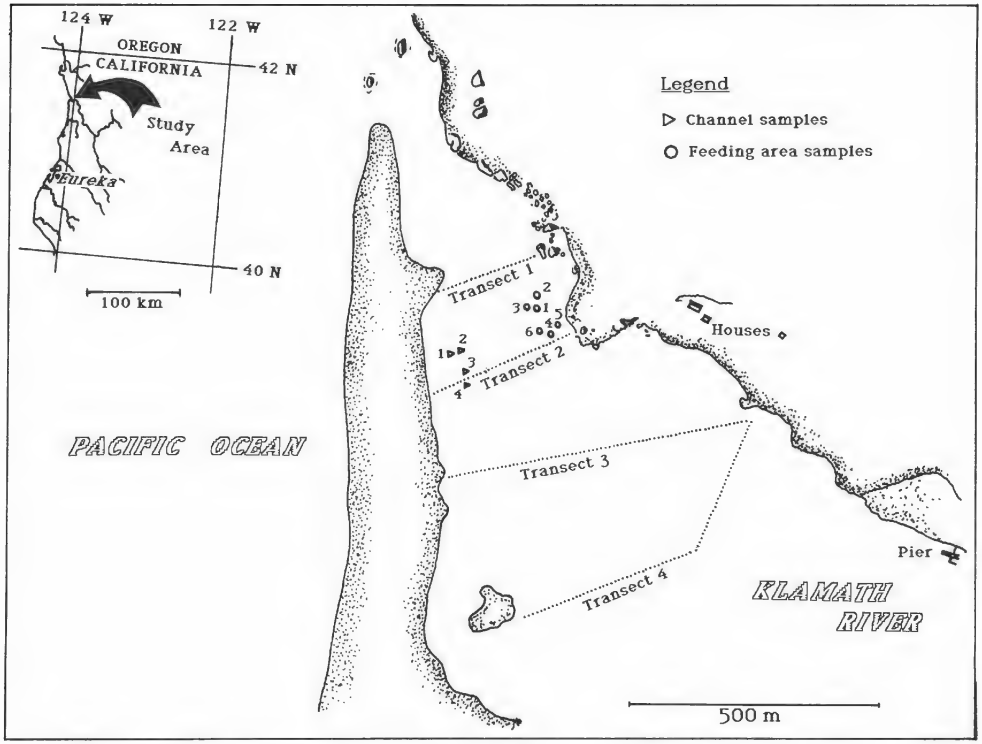

Figure 1. Study area. The mouth of the Klamath River.

second group of six cores ("feeding area samples"; 0.0042 square meters each) was collected in an area of observed gray whale feeding. Two of these samples were obtained within recent feeding excavations ("disturbed area samples"). The remaining four of the feeding area samples were taken from undisturbed areas of the tube mat and are so designated.

We preserved all samples in 5% buffered formaldehyde, and washed them over a 1.0 mm mesh screen. Infaunal organisms were removed from tubes and sediment, counted, and stored in 70% ETOH. Biomass was measured as wet weight of total infaunal organisms.

Results and Discussion

General Observations

The juvenile gray whale was initially observed in mid-July of 1989 and was seen intermittently in the Klamath as late as March of 1990, suggesting that it spent the winter in the river as well. Gray whales have been observed along the coast of northern California during the summer for years (Dohl *et al.* 1981, Mallonee 1991). To our knowledge, however, this is the first published account of an identified individual gray whale spending the summer off northern California.

We saw the gray whale daily spending long undisturbed periods foraging in the shallow waters of the estuary, usually within one-half mile of the mouth. It could move in and out of the river mouth, independent of tidal stage. It maintained a reasonably uniform series of movements within the estuary, usually swimming southward along the sand spit, then crossing the channel and making its way to the north along the opposite shoreline. The animal also made smaller loops at various places in the estuary, concentrating its feeding efforts in specific locations.

During a total of 47.5 hours of observations, the animal spent 58.1 percent of its time feeding,

29.3 percent traveling, primarily between feeding areas, 6.5 percent resting and 6.1 percent on other behaviors. The largest portion of feeding (52.5%) was concentrated along the northeast shore of the estuary, while feeding along the sand spit (36.2%) and elsewhere in the estuary (12.3%) was less common.

Respiration data collected on several different occasions revealed a remarkably consistent pattern of breathing and diving. Typically, a series of two to four respirations (blows) with relatively short blow intervals would be followed by a dive ranging from two to five minutes. The number of blows per surfacing, the surface interval, and the dive lengths showed little variation during the course of the study.

Benthic Survey

The underwater survey of the estuary bottom, ranging from 1 m depth near shore to 6 m depth in mid-channel, revealed a very extensive covering of amphipod tubes. The substratum generally consisted of fine sand or silt with occasional zones of sand and rocks. In the deeper channel sediments, amphipods were present though their tubes were least evident. An examination of the feeding area (depths of 2.5 m to 3.5 m) revealed several recent gray whale feeding excavations as well as older pits being recolonized by amphipods. The recent pits were characterized by relatively clean, straight edges, exposed amphipod tubes along the sides, and few tubes within the pit. The sizes and shapes of the excavations (Figure 2) were similar to those observed in Pachena Bay, Vancouver Island, B.C. (Oliver *et al.* 1984) and in the Bering Sea (Nerini 1984). Depths of the excavations ranged from five to ten centimeters.

Core Samples

Analysis of the core samples (Table 1) showed that the infauna were strongly dominated by *Corophium spinicorne,* with a small number of other amphipods, mostly of the genus *Anisogammarus.* Isopods and mysids were also present in very low numbers. The tube-mat density (amphipods per square meter) was highest in the undisturbed part of the feeding area. In the disturbed area, two samples were taken within recent feeding excavations and contained very few amphipods.

Mean densities and biomasses for the amphipod tube mats in the Klamath River estuary are comparable to those reported for other places where gray whales feed (Table 1). Although the corophid amphipods in the Klamath have a similar biomass to that of the ampeliscid amphipods in the Bering Sea, they are much smaller. Mills (1967) reports lengths of 12 to 20 mm for adult *Ampelisca macrocephala,* whereas we found *Corophium* ranging from 2 to 9 mm. Smaller sizes would imply a greater surface-to-volume ratio, suggesting that a larger portion of the Klamath amphipod biomass may be chitinous exoskeleton. As

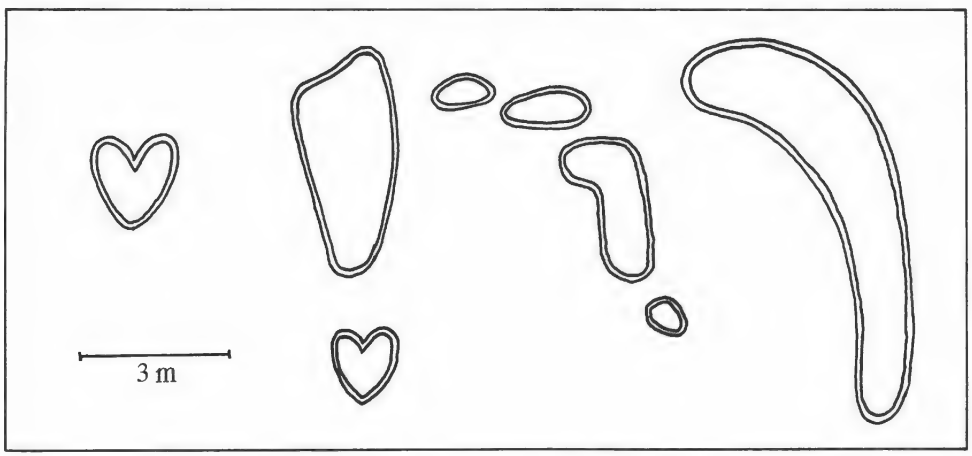

Figure 2. Gray whale feeding excavations observed in the mouth of the Klamath River located near the end of Transect 2 at depth of 2.5 meters.

TABLE 1. Mean infaunal densities (organisms/m²) and biomass (grams/m²) for this study as compared to other dense amphipod communities associated with gray whale feeding.

Location	Klamath Channel edge mean	(SD)	Klamath–Feeding area* Undisturbed mean	(SD)	Disturbed mean	(SD)	Bering Sea (Oliver *et al.* 1983)** mean	(SD)	Pachena Bay, B.C. (Oliver *et al.* 1984)** mean	(SD)
Sample size	n = 4		n = 4		n = 2					
Corophium	50,700	(7,930)	84,300	(21,400)	7,260	(8,920)				
Other amphipods	7,300	(1,570)	5,540	(3,660)	476	(673)				
Isopods	100	(115)	1,370	1,680)	0					
Mysids	100	(200)	0		0					
Nematodes	850	(1,570)	950	(1,440)	476	(673)				
Total infauna	59,050	(8,900)	92,160	(18,900)	8,210	(10,300)	28,923	(8,041)	118,583	(45,220)
Total biomass (g/m²)	221	(23)	446	(105)	34	(45)	482	(226)	197	(71)

* Area of cores: channel edge–0.0050/m²; feeding area–0.0042/m². Volumes of samples are not calculated because, in all cases, the depth of the core penetrated to at least three centimeters below the level inhabited by amphipods.
** It should be noted that Oliver *et al.* washed their samples over a 0.5 mm mesh screen, whereas we washed the Klamath River samples over a 1.0 mm mesh screen. Because the organisms involved are relatively large and tend to remain in or cling to the amphipod tubes, this difference in screen mesh is not likely to affect the comparisons made here significantly.

lipid content is known to be quite variable in arctic amphipods (Percy and Fife 1981), determining the lipid content of corophids would be helpful in assessing the food value of the amphipod mats in the Klamath estuary.

The correlation between the intensity of the whale's feeding activity and the density of the corophid tube mats suggests that the whale may have been feeding selectively in areas with the greatest density of amphipods. Similar conclusions have been drawn from the observations of gray whale feeding in other areas (Oliver *et al.* 1984). It is also clear that the whale was very effective at removing the amphipods from the bottom as shown by the dramatically reduced amphipod densities within the excavations.

Conclusion

Our discovery of a gray whale feeding in a northern California estuary during the summer provides further evidence of a potentially increasing use of tertiary feeding grounds (areas other than the Bering and Chukchi seas), south of Vancouver, B.C. (Kim and Oliver 1989). As these animals rely, almost exclusively, on the food that they are able to obtain during the summer, an expansion of their summer range is dependent upon the presence of additional feeding areas where epibenthic or infaunal prey is available to them. It is very encouraging to learn that these animals can utilize estuaries, such as the Klamath River in California.

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Book Review

Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. Technical Coordinators: Leonard F. Ruggiero, Keith B. Aubry, Andrew B. Carey, Mark H. Huff (U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon. General Technical Report PNW-GTR-285)

The most significant natural resource issue in the United States faced by the current generation concerns the fate of the remaining old-growth Douglas-fir forests scattered in largely isolated patches across the Pacific Northwest landscape. Prior to settlement in the region, it is estimated that old-growth forests blanketed approximately 10 million hectares. As a result of escalating development and intensive logging, only 10 percent of these majestic forests are believed to remain. At the heart of the controversy is whether old-growth forests are unique forested environments with distinctive floral and faunal components that should be nurtured and preserved for future generations.

In 1981, the U.S. Forest Service chartered the Old-Growth Forest Wildlife Habitat Research and Development Program to examine in detail the interrelationships between wildlife and the dwindling old-growth resource, and to compare the species assemblages found with those of younger forests. The objective was to provide credible, scientific information to help guide future forest management decisions on public lands, the major stronghold of remaining old-growth forests. After years of intensive research undertaken throughout the Douglas-fir and mixed-conifer regions of Oregon, Washington, and northern California, a public symposium was held in Portland, Oregon in March 1989 to present the major findings of the research effort. *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests* is the published proceedings of that symposium.

This book is a compilation of 27 research papers organized into eight sections. The first three sections set the scene and start the volume off at an energetic pace. *Part I* contains background papers that discuss events leading up to the Old-Growth Program, its purpose, and the general research sampling design. *Part II* provides historical information about Pacific Northwest Douglas-fir forests including their origin, fire history, and current fragmentation problems, in addition to articles on old-growth inventories and ecological definitions. *Part III* is dedicated to evaluations of the composition, function and structure of old-growth forests compared with earlier successional states.

Wildlife is the primary focus of the next few sections, but avoidable repetitious information rendered in consecutive articles results in tedious reading. Regional patterns of breeding and wintering bird communities, small mammal communities (including bats), and amphibians in Douglas-fir forests in Oregon and Washington are examined in detail (*Parts IV through VI*); each contributing author describes the results of vertebrate surveys throughout the study range and relates species diversity and abundance to forest structure. Several summary articles that compare results across locations are particularly welcome.

A variety of mixed-conifer forest community studies undertaken in northern California and southern Oregon are combined in a single section (*Part VII*); these articles are generally more directed and concise than previous ones. The book concludes with informative and eloquently written overview and summary articles that highlight significant results of the old-growth research effort and underscore the applicability and limitations of the data (*Part VIII*).

In reading this compendium of research results, one becomes immediately and acutely aware of the magnitude of the research endeavor that occurred under the auspices of the Old-Growth Program. Unfortunately, only unmanaged forests were examined in these studies as funding was insufficient to address the formidable issue of similarities between natural versus managed forests. It is critical, however, that this subject be pursued in the immediate future if our intensively used National Forests are to maintain viable populations of all native vertebrates as directed by the National Forest Management Act of 1976. The research presented in this volume will provide the solid foundation upon which these future studies can be built.

It will be disappointing to some that the major finding of the Old-Growth program is that species composition of old-growth forests varies little from earlier successional stages of naturally regenerated

forests. The reason proposed for this similarity is the high degree of structural overlap between old-growth and younger unmanaged forests due to a complex of old-growth features such as snags and remnant large-diameter trees retained after catastrophic events such as fire; high structural overlap seems to equate with high species similarity, and the reader is exposed to variations of this sentiment in almost every article. Under current management practices, forests tend to have reduced structural diversity, thus many authors offer suggestions for manipulating managed forests to emulate complex old-growth features.

Although species composition of unmanaged forests is similar across forest ages, species abundance is not. The organisms studied were consistently more numerous in old-growth forests compared to younger seral stages suggesting that old-growth has a higher carrying capacity per unit area for a wide range of species. This finding contributes significantly to the overall conclusion that old-growth forests are unique and indispensable.

Because of the massive scope of the project, not all aspects of the Old-Growth Program are included in this publication. It is unfortunate, however, that detailed spotted owl research results are omitted. Although it is stipulated in the introductory section that biological communities rather than individual species would be emphasized in the text, failure to provide significant information on this high profile species appears blatantly evasive. Inclusion of research information on the owl, the most studied animal in old-growth forests, could only have strengthened the collective contention of the researchers that old-growth forests are indeed unique.

Although the compilation of this wealth of information into one text was largely a success, a different approach to the organization of the research results could have reduced repetition to a minimum and would have substantially increased the reading pleasure of the book. Fluid reading is further stymied by a glossy paper stock that reflects light and a peppering of editorial oversights including but not limited to incomplete table and figure descriptions and misplaced hyphens. Most errors are minor irritations, however, with the exception of one article in Part II where Soulé is incorrectly cited an unforgivable number of times. Finally, the pervasive use of the term "association" to describe "correlation" will likely provoke those with a statistical orientation.

When one considers the massive effort behind the Old-Growth Forest Wildlife Habitat Research and Development Program, it is easy to pardon the few problems of content and style in the published results. *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests* chronicles landmark research into the structure, function and composition of unmanaged forests and should be read and absorbed by all who work in forest management as well as by those concerned with the future well-being of our taxed forest resource. This publication has the potential to foster a new awareness of the multifaceted attributes of forested systems, to motivate the scientific community to expand upon the research initiated here, and to inspire forest stewards to undertake innovative measures to benefit wildlife while maintaining forest productivity. Great strides will be made in balancing demands on our forests if these endpoints are realized.

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Page Charges—Page charges are currently $60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon the manuscript's being accepted for publication.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½ x 11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures);* provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1990).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

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The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $14 per year ($8 per year for students). Institutional memberships, $40 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

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Announcements

1993 Annual Meeting of the Northwest Scientific Association

The Northwest Scientific Association will hold its 66th Annual Meeting on March 25-27 at Eastern Oregon State College, La Grande, Oregon. Symposium topics will include "Research and Management of Bats in the Northwest," "Cumulative Effects of Land Management Practices on Anadromous Salmonids," and "Status of Forest Health Issues in Northeast Oregon." Contributed paper sessions will occur in the areas of Botany, Forestry, Geology, Range Science, Aquatic Ecology, and Zoology. The banquet speaker (March 25) will be Jack Ward Thomas. A juried show of wildlife art will be open throughout the meeting.

Northeast Oregon offers a rich diversity of ecosystems, and field trips will be scheduled to take advantage of this. Field trips may also supplement the symposia.

The deadline for abstract submission is February 1, 1993. A program listing paper titles, authors, and scheduled times will be mailed to members in early March. Abstracts will be available at the meeting and will be published in the May issue of *Northwest Science.* Students are strongly encouraged to participate.

For additional information regarding the meeting, contact Dr. Karen Antell, Program Chairwoman, or Dr. Burr Betts, NSA President, Biology Department, Eastern Oregon State College, La Grande, OR 97850-2899; (phones: 503-962-3610 and 503-962-3330, respectively).

1993 Student Research Grant

I. ELIGIBILITY

Applicants must be regular members of the Northwest Scientific Association. *Northwest Science* (the journal of the society) has information for joining the society.

II. PREPARATION OF THE PROPOSAL

A cover page should be provided to include: Name and address of applicant, associated institution, name of major professor/advisor, degree program, year in school, and amount of money requested (maximum of $500).

The proposal should include: Title, Statement of Justification, Methodology/Experimental Design (including methods of analysis), and detailed budget (on separate page).

The proposal length should be no more than three (3) *double spaced* pages (not including budget page).

Proposals are due on or before **MARCH 1, 1993** and should be sent to:

Dr. R. Gerald Wright
Department of Wildlife Resources
University of Idaho
Moscow, ID 83843
Phone (208) 885-7990

Grants will be awarded at the annual meeting of the Northwest Scientific Association held in La Grande, Oregon, March 24-26, 1993.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences and social sciences. Monies should be used only to support research activities of the student. It is expected that students will report results of their research at a future NSA meeting.

Howard A. Gard, Battelle, Pacific Northwest Laboratory, Richland, Washington 99352

Resource Distribution and Prehistoric Utilization of Southern Oregon's Coastal Islands

Abstract

The portion of the Oregon coast extending from Cape Blanco south into California has long been recognized as a unique physiographic region, resulting in distinct prehistoric subsistence and settlement patterns when compared with other coastal areas. Several researchers have proposed models emphasizing littoral adaptive strategies for this region but have failed to outline the type, distribution, and abundance of subsistence resources available to prehistoric populations. I propose that the abundant offshore rocks and islands along this section of coast served to concentrate marine resources and were, therefore, of economic importance to prehistoric populations. In particular, I demonstrate that 1) rocky coastlines are highly productive environments providing a variable, abundant, year-round food supply of immediate use to humans; 2) this high productivity can be directly related to the increased habitat provided by offshore rocks and islands; and 3) these offshore resources were utilized by prehistoric peoples. A combination of archaeological testing of one offshore island site and a sample survey of selected rocks and islands provides evidence of prehistoric utilization of offshore features. A majority of settlement/subsistence models tend to use observed site distributions to infer a region's relative biotic productivity, an inaccurate approach. This paper illustrates an alternate approach by determining the resources provided by a rocky coastline, inferring human use of those resources, and collecting archaeological evidence of that use.

Introduction

Archaeological research along the Oregon coast has been dominated by models emphasizing littoral adaptive strategies (Lyman and Ross 1988, Minor and Toepel 1983, Gould 1976, Draper 1988). Support for these models has been based principally on site distribution, or, in the case of Lyman and Ross (1988), on the high productivity of estuaries. While some notice has been given to latitudinal variation in coastal morphology, little attention has been paid to variation in the distribution, density, and variety of subsistence resources between the southern and northern portions of the coast. Draper's (1988) is the only model which directly addresses the unique rocky character of the southern Oregon coast and suggests that this region supported large, sedentary populations. He found that residential sites were concentrated within the marine habitat, with some sites less than 3 km apart. Sites also appeared to be associated with highly productive physical settings, the most frequently occupied being stream mouths and bluff/cliff areas (Draper 1988:318). Estuarine habitats exhibited the lowest site density. Draper infers a settlement pattern of sedentary villages located in areas where resources were predictably aggregated at known times of the year, with subsistence resources being harvested within the village's immediate vicinity. Because prime village locations (those in proximity to several habitats) are few, these locales exhibit nearly continuous occupation through time (Draper 1988).

All other models describe a land-use system where winter villages were occupied for a considerable portion of the year, with task groups moving annually to areas having predictable, concentrated resources. These locales could exist up to fifteen miles from the main village and were used for resource harvest and processing before transportation back to the main winter village. This process suggests a heavy wintertime reliance on stored foods and the need to maintain a large catchment area (Gould 1976, Lyman and Ross 1988, Minor and Toepel 1983).

Draper's work suggests that rocky coasts are more productive in terms of usable foodstuffs than previously considered. In this paper I propose that rocky coastlines are highly productive settings capable of supporting Draper's settlement/subsistence model. The offshore rocks and islands served to attract and concentrate subsistence resources important to indigenous hunter-gatherers and may account for these higher observable site densities. I provide the first evidence for prehistoric utilization of offshore islands there.

Instead of using site distribution and/or density as an implied measure of a region's productivity, I focus on the availability and distribution of subsistence resources and from this information suggest the most likely settings for resource extraction. This appears to be a promising tool for deciphering prehistoric land use patterns.

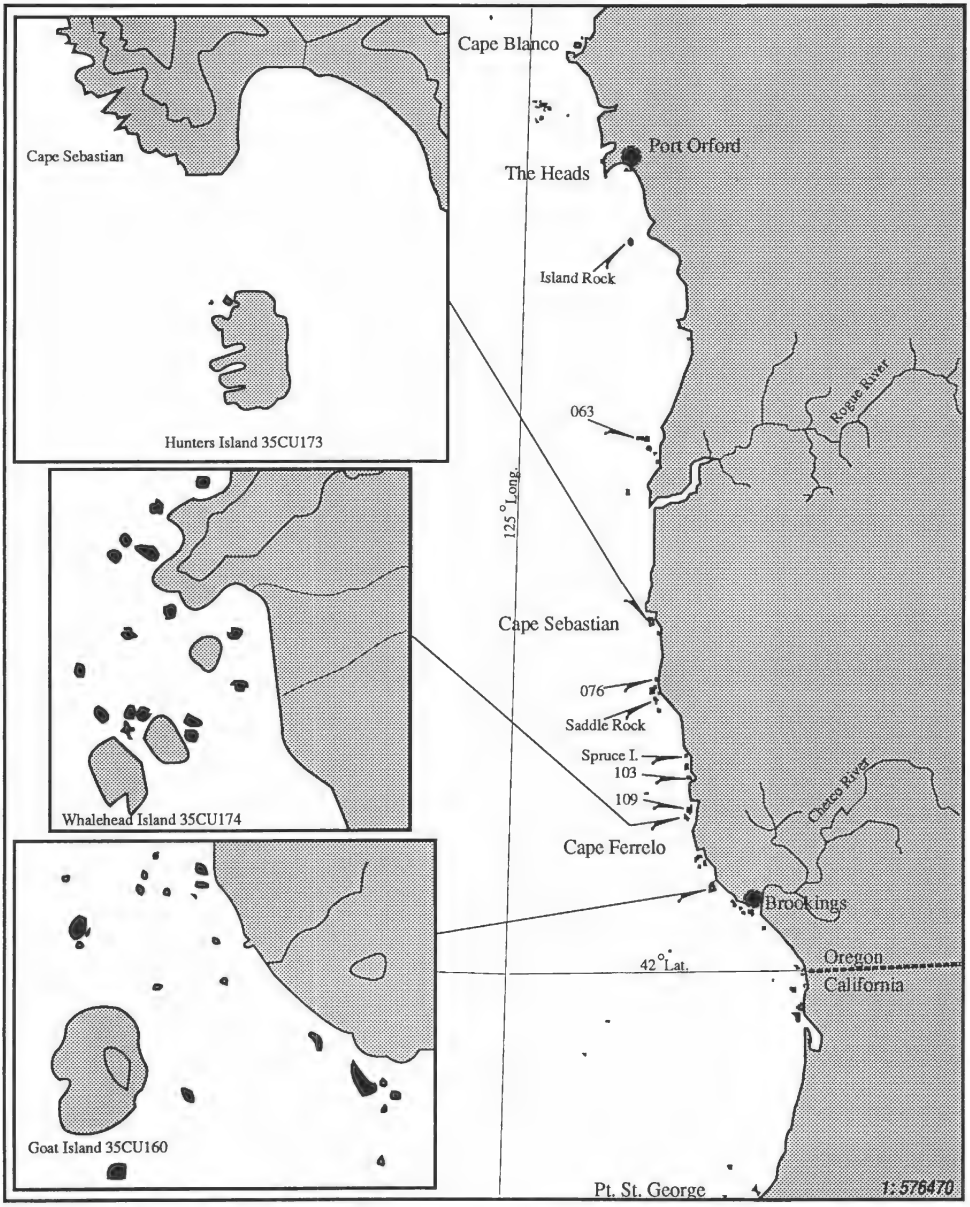

Figure 1. Study area with insets of offshore islands containing archaeological sites.

Setting

The coastline from Cape Blanco south into northern California is physiographically distinct from the remainder of the Oregon coast (Figure 1). Its unique geologic origin is reflected in the character of the coastline. The southwestern corner of Oregon and the northwestern corner of California fall within the Klamath Mountain region of the

Pacific border province (Fenneman 1931). Bounded on the north and south by the Oregon and California coast ranges respectively, on the east by the Cascade Mountain ranges, and by the Pacific Ocean along the western edge, the Klamath Mountains have twice the relief of the Coast Ranges and more rugged topography than the Cascade Range (Dicken 1965). Canyons tend to be narrow and are separated by east/west trending, knifelike ridges, with relief ranging from 600 to 1,500 m (Baldwin 1976). The coastline is rugged and rocky, with steep sea cliffs, narrow, coarse gravel beaches (when they occur), and numerous offshore islands and rocks (Dicken 1961). Extensive, well-developed marine terraces occur throughout the region.

With the exception of the Rogue River, which has its headwaters in the Cascade Mountains, the numerous coastal streams and rivers originate in the Klamath Mountains. Typically, they have a dendritic drainage pattern, relatively short courses, steep gradients, and a low sediment load (Oceanographic Institute of Washington, [OIW] 1977). The Rogue and Chetco rivers are the largest drainage systems of the region and are the only rivers with significant estuaries (U.S. Army Corps of Engineers [ACE] 1971). Recent tectonic uplift within the Klamath Mountains has resulted in downcutting and stream channelization. Tidal influence rarely extends inland more than 1.5 km (OIW 1977). This can be contrasted with broad, drowned river valleys of the northern coast, with their 24 to 32 km inland tidal influence. The southern coast comprises over one-fifth of the total coastline of the state, yet contains only 2% of the estuarine shoreline.

In general, before the arrival of Euro-Americans, coastal cliffs, headlands, and islets were covered with low grasses, sedges, and herbs, with height and density of vegetation increasing inland and culminating in a dense climax forest. The diverse, rich plant communities found within the study area provide abundant habitat for terrestrial wildlife (Franklin 1981), while the rugged, rocky coastline contributes to a plethora of marine organisms, waterfowl, and seabirds. Coastal streams support anadromous fish and provide fresh water habitat.

Rocks and Islands of Southern Oregon

One of the unique features of the coast of southern Oregon is the preponderance of offshore rocks, sea stacks, and islands. While often cited as contributing to the beauty of the area, no archaeologist has previously considered that these features may have had a direct influence on overall productivity and resource abundance. I define offshore islands and rocks as those surrounded by water even during minus tides, a critical distinction, allowing these features to provide essential habitat components. Further, to be considered an island rather than a rock, a feature must exhibit vegetation or soil development. Onshore islands and rocks, on the other hand, are those accessible dryshod at low tide. That these onshore features were utilized by prehistoric inhabitants has been documented, but they represent a separate habitat assemblage and are not considered here.

Gould (1966, 1976) documents prehistoric utilization of some rocks off Point St. George. A large sea lion rookery was exploited, and cormorant fledglings were harvested from nearshore rocks. Several researchers (Berreman 1944, Chase 1873, Ross 1977, Schumacher 1877a, 1877b) note the association of offshore rocks with large mainland village sites. Heflin (1966:162) cites an unpublished work by T. T. Waterman stating that an island known as *Maski,* now called Hunters Island, was used for hunting otters and collecting cormorant and gull eggs. Heizer (1951) reports an island used for religious purposes off of Patrick's Point, California. Draper (1988:321) notes the presence of four archaeological sites on coastal islands, considering them extensions of headland ecological communities. Given the placement of three of these sites—Eagle Rock (35 CU 94), Harris Beach (35 CU 80), and Zwagg Island (35 CU 94), this interpretation is probably correct since these are onshore rocks, some of which are surrounded by water only at extreme high tides. Of these, Goat Island (35 CU 160) is the only true island, isolated by water year-round and providing unique habitat for plant and animal species.

Coastal Productivity

The southern coast of Oregon is a highly productive region. Intense upwelling provides essential nitrogen and phosphorous for phytoplankton development from July through September (Fisher 1970, OIW 1977). Upwelling is more pronounced south of Cape Blanco, compared to the remainder of the Oregon coast, due to the narrower continental shelf and the orographic effect of the Klamath

Mountains, which result in intensified offshore winds (Fisher 1970, Ramberg 1970). Abundant phytoplankton provides a rich food base, while the offshore rocks and islands provide great habitat diversity, increasing the coastline's topographic complexity by increasing the linear area of shoreline, reducing wave shock, creating a mosaic of substrates, and providing more horizontal living space for zonal animals. These factors account for the greater diversity and abundance of animals associated with this section of coast (Ricketts *et al.* 1985:15, Williams and Monroe 1976:13).

Animals of greatest economic importance to prehistoric people associated with offshore rocks and islands are shellfish, principally California mussels (*Mytilus californianus*) (Barner 1981, Berreman 1944, Erlandson 1988, Gard 1990, Gould 1976, Greengo 1952, Heflin 1966, Winterhalder 1981, Yesner 1980), pelagic and demersal fishes which are attracted to the intertidal areas (Gard 1990, Zontek 1983), sea birds, particularly those that use the islands as breeding sanctuaries (Gard 1990, Gould 1966, 1976), and marine mammals (Berreman 1944; Gard 1990; Gould 1966; Heflin 1966; Hildebrandt 1984; Lyman 1988, 1989, 1991; Rambo 1978; Ross 1977). A list of species associated with offshore rocks and islands and their surrounding waters is provided in Table 1.

The coastal rocks and islands are the central element in a dynamic system. As with all ecosystems, there is a high degree of interrelatedness. Dense bird colonies develop because rocks and islands provide secure nesting habitat, while offshore waters provide abundant food for rearing broods. In turn, bird guano, high in nitrogen and phosphorus, accumulates on the rocks and is subsequently washed off by wave action and heavy winter rains, thereby enriching the surrounding waters and furthering plankton production (Mizutani and Wada 1988, Zelickman and Golovkin 1972). A similar cycle probably occurs around sea mammal rookeries and intensively used haulouts. Planktophageous fishes are attracted to rocks and islands by abundance of food and are, in turn, preyed upon by sea birds, sea mammals, and carnivorous fish. High predation upon plankton-consuming fish makes more plankton available to intertidal and benthic invertebrates, whose increased availability supports other consumers such as oyster catchers and sea otters. Sea otters have a direct effect upon their environment by preying upon sea urchins (*Stronglyocentrotus spp.*), thereby fostering the development of kelp beds, yet another productive habitat (Mate 1981).

Island Archaeology

Optimal foraging theory predicts that 1) people choose food to maximize benefits (e.g., gather maximum net energy per time allotment), or 2) they hunt and gather in such a manner as to minimize costs, especially the time required to meet their energetic requirements (Pulliam 1981:65). Employing either criterion, offshore rocks and islands should have been exploited since abundant, diverse, concentrated resources provide both maximum return and minimum time expenditure. To evaluate this hypothesis, I conducted archaeological testing on Goat Island (35 CU 160), the only previously known offshore site on the Oregon coast (Gard 1990), and performed an offshore survey of accessible rocks and islands.

Goat Island (35 CU 160)

Goat Island is an 8.5 hectare, vegetated island located 600 m offshore and approximately 5 km northwest of the Chetco River outlet (Figure 2). Rising over 60 m from mean sea level, the perimeter of the island consists of sheer cliffs. Unlike any other island along the southern coast of Oregon, a small sand beach is located on the lee side, greatly facilitating island access.

This island and others along the Oregon coastline are administered by the United States Fish and Wildlife Service (USFWS) and comprise the Oregon Islands National Wildlife Refuge. Goat Island is managed for use by colonial nesting sea birds and as a wintering habitat for migratory waterfowl, especially the dusky Canada goose (*Branta canadensis occidentalis*) and the endangered Aleutian Canada goose (*B. c. leucopaeia*). Because of Goat Island's refuge status, access is strictly controlled, as is the case with all Oregon coastal islands, and must be timed to avoid conflict with the use of the islands by birds. The goal of archaeological sampling was to illuminate the role of the site in prehistoric economies by determining its integrity, function, content, chronological placement, and season of use. (See Gard 1990 for complete discussion.) Two excavators conducted testing with assistance from the USFWS Coastal Biologist, who provided transportation and monitored the excavations to ensure minimal disturbance of wildlife

TABLE 1. Representative Species Found on the Southern Oregon Coast.

BIRDS

Taxon	Common Name
Haematopus bachmani	Pacific oyster catcher
Larus occidentalis	Western gull
*Oceanodroma furcata**	Fork-tailed storm petrel
*Oceanodroma leucorhoa**	Leach's storm petral
Phalacrocorax auritus	Double-crested cormorant
Phalacrocorax pelagicus	Pelagic cormorant
Phalacrocorax penicillatus	Brant's cormorant
Uria aalge	Common murre
*Cepphus columba**	Pigeon guillemot
*Frateroula corniculata**	Tufted puffin
*Cerorhinca monocerata**	Rhinoceros auklet
*Ptychoramphus aleuticus**	Cassin's auklet
Branta canadensis	Canada Goose

*Burrow Nester

MOLLUSCS/CRUSTACEANS

Taxon	Common Name
Ostrea lurida	Native oyster
Tresus nuttalli	Gaper clam
Clinocardium nuttalli	Cockle
Macoma nasuta	Bentnose clam
Mya truncata	Softshell clam
Protothaca staminea	Littleneck clam
Saxidomus giganteus	Butter clam
Siliqua patula	Razor clam
Tresus capax	Horse clam
Mytilus californianus	California mussel
Cryptochiton stelleri	Gumboot chiton
Katherina tunicata	Black chiton
Olivella biplacata	Purple olive
Searlesia dira	Dire whelk
Mitella polymerus	Gooseneck barnacle
Balanus cariosus	Horse barnacle
B. glandulus	Acorn barnacle
Cancer magister	Dungeness crab
C. productus	Red rock crab
Stronglyocentrotus spp.	Sea urchin

FISH

Taxon	Common Name
Clupea harengus pallasi	Pacific herring
Sardinops sagax	Pacific sardine
Thunnis alalunga	Albacore
Engraulis mordax	Northern anchovy
Rhacohilus vecca	Pile perch
Amphistichus rhodoterus	Redtail surfperch
Cymatogaster aggregata	Shiner perch
Embiotoca lateralis	Striped sea perch
Hyperprosopon argenteum	Walleye surfperch
Phanerodon furcatus	White sea perch
Scorpaenidae	Rockfishes
Ophiodon elongatus	Lingcod
Scorpaenichthys marmoratus	Cabezon
Enophrys bison	Buffalo sculpin
Hemilepidotus spp.	Irish lords
Hexagrammos stelleri	White spotted greenling
H. decagrammus	Kelp greenling
Raja binoculata	Big skate
Psettichthys melanostictus	Sand sole
Parophrys vetulus	English sole
Platichthys stellatus	Starry flounder
Anarrhichthys ocellatus	Wolffish
Galeorhinus zyopterus	Soupfin shark
Squalus acanthias	Spiny dogfish
Thaleichthys pacificus	Eulachon
Lampetra tridentata	Pacific lamprey

SEA MAMMALS

Taxon	Common Name
Eumetopias jubata	Steller sea lion
Zalophus californianus	California sea lion
Phoca vitulina	Harbor seal
Callorhinus ursinus	Northern fur seal
Enhydra lutris	Sea otter
Mirounga angustirostris	Northern elephant seal

and damage to nesting habitat. A single 1 x 2 m test pit was dug in 10 cm arbitrary levels, with all excavated soils bagged by level for water-screening through graduated meshes (ranging from 6 mm to 1.5 mm) at the Oregon State University archaeology laboratory. A total of .4 m^2 of soil was excavated. Sediments are a dark brown, loamy clay, containing approximately 50 percent shell, by volume. The shell is extremely fragmented, with average pieces about 5 mm in diameter. Soils are extensively mixed, attributable to considerable bioturbation by a myriad of burrowing invertebrates, an unknown salamander species, and, particularly, the activity of burrow-nesting storm petrels, tufted puffins, and auklets. Burrow densities reach a maximum of 50 per m^2 (Lowe pers. comm. 1989), limiting the potential for conducting intrasite spatial analysis at some later date. Furthermore, although the test pit was excavated in 10 cm levels to provide vertical control, disturbance limits the utility of these controls. Therefore, the materials discussed are treated as a single analytical unit.

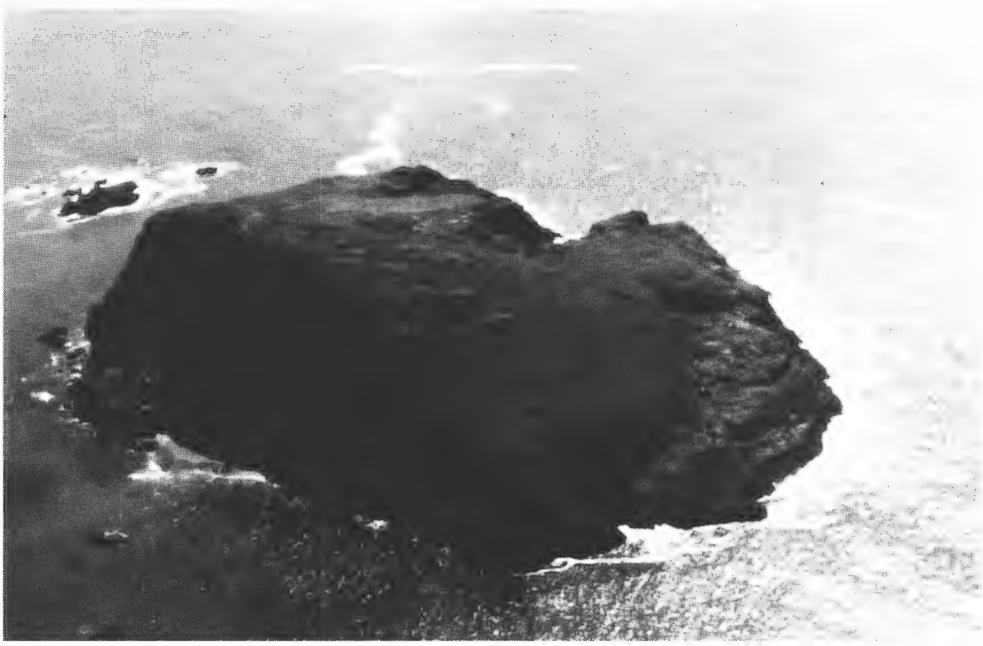

Figure 2. Aerial view of Goat Island, looking southwest. Photo by R. Lowe, USFWS.

Cultural materials extend to a depth of 30-35 cm below surface. Charcoal recovered from a deflated hearth feature yielded a radiometric date of 880 ± 50 B.P. (Beta 31003), which places utilization of the site within the late prehistoric period (Lyman and Ross 1988).

The most abundant faunal remains recovered are shellfish, totaling 5.459 kg dry weight (Table 2). California mussel comprises more than 80 percent of the shell. The rock margins around the island are thickly covered with these molluscs, as well as with gooseneck barnacle. Although gaper and littleneck clams are generally considered bay/estuary species, they can be found on the island along its beach or on the mainland directly across from the island. Chitons and barnacles are common residents. The dire whelk, represented by a single shell, also is found on rocky shores with quiet, protected waters but is usually associated with bay/estuary habitats. There are four olivella specimens missing distal end spirals, which may be beads (Moratto 1984).

Marine fish are the second most abundant taxa in the sample (Table 2). All fish identified to genus are inhabitants of rocky shores and kelp beds and/or can be found in nearshore waters. The surfperches, which cannot be confidently identified to genus due to the skeletal similarities of related genera, are probably striped sea perch (*Embiotoca lateralis*) since it prefers rocky shores and kelp beds.

Most of the bird remains identified to species (Table 2) belong to storm petrels, with tufted puffins second most abundant. Because of normal fledgling mortality and the burrowing habits of the two species, it is probable that their remains have been naturally incorporated into the site, an interpretation supported by a high percentage of fresher looking bone in the faunal sample. Three bone fragments cannot be attributed to natural deposition: a proximal humerus head and a distal coracoid end from a pelican-sized bird and a medial ulna fragment from a cormorant-sized bird. These are too fragmentary for species determination but appear to be concurrent in age with the mammal bone believed to be coincident with human occupation.

TABLE 2. Faunal remains from Goat Island (35 CU 160), listed in order of relative abundance.

SHELLFISH

Family	Taxon	Common Name	NISP/MNI
Mytilidae	*Mytilus californianus*	California mussel	+
Mactridae	*Tresus nuttallii*	Gaper clam	+
Veneridae	*Protothaca staminea*	Littleneck clam	+
Acanthochitonidae	*Cryptochiton stelleri*	Gumboot chiton	+
Mopaliidae	*Katherina tunicata*	Black chiton	+
Olividae	*Olivella biplacata*	Purple olive	+
Buccinidae	*Searlesia dira*	Dire whelk	+
Lepadidae	*Mitella polymerus*	Gooseneck barnacle	+
Balanidae	*Balanus sp.*	Acorn barnacle	+

FISH REMAINS

Family	Taxon	Common Name	NISP/MNI
Scorpaenidae	*Sebastes spp.*	Rockfish	9/4
	Sebastes siminiatus	Vermilion rockfish	2/2
	Sebastes melanops	Black rockfish	25/4
Embiotocidae	*Embiotoca lateralis ?*	Striped sea perch	7/1
Cottidae	*Enophrys bison*	Buffalo sculpin	1/1
Hexagammidae	*Hexagrammos decagrammus*	Kelp greenling	2/1
Unidentified fish bone fragments			609

AVIAN REMAINS

Family	Taxon	Common Name	NISP/MNI
Hydrobatidae	*Oceanodroma sp.*	Storm petrel	76/10
Alcidae	*Frateroula corniculata*	Tufted puffin	2/1
Unidentified (Pelican-sized bird)			2
Unidentified (Cormorant sized-bird)			1
Unidentified[1]			71

[1]The majority of these unidentifiable bird bone fragments appear to be eroded or from immature birds, lacking epiphysis.

SEA MAMMAL REMAINS

Family	Taxon	Common Name	NISP/MNI
Otariidae	*Eumetopias jubatus*	Steller's sea lion	1/1
	Callorhinus ursinus	Northern fur seal	1/1
Phocidae	*Phoca vitulina*	Harbor seal	1/1
Unidentified sea mammal frags			86

Mammal bone comprises the remainder of the faunal material recovered (Table 2), with only three elements identifiable to taxon (Gard 1990). Apparent butchering marks were found on one of the rib fragments, suggesting human activity.

The recovery of artifacts provides firm evidence of human utilization of the island, but the sample is too small to provide any definitive indication of specific tasks performed. Recovered debitage indicates that stone tool production and/or maintenance occurred on site. With only one exception, locally available material was utilized (Gard 1990). Nine artifacts were recovered, consisting of projectile points (Figure 3), blanks, preforms, retouched flakes, and bone tools (Gard 1990). Two stemmed projectile points are very similar to protohistoric specimens recovered in the interior Klamath Mountain region (Aikens 1986:114). This is consistent with the 880 ± 50 B.P. date obtained from the radiocarbon sample. A triangular, concave-base point is stylistically similar to composite harpoon tips described by Gould (1966:56) but is too small

Figure 3. Projectile points recovered from the Goat Island Site, 35 CU 160.

to be a harpoon tip according to criteria established by Lyman *et al.* (1988). The points indicate extractive tasks were carried out on the island, an interpretation independently confirmed by the faunal remains.

With the exception of the puffin and petrel remains, faunal material appears to have been incorporated into the site as a result of human activity, thereby providing an indication of the range of exploited species. Some shellfish could have been deposited on the island by sea birds, but the quantity, presence of carbonized shell, and preferential selection of species suggest a human agent. The sheer cliffs which form the island perimeter would prevent the natural deposition of sea mammal bones at the site. Finally, none of the fish bone exhibits any evidence of digestive corrosion, thereby discounting the possibility that the bone was brought to the site in the stomachs of harvested sea lions, and the majority of the fish are too large to have been transported by birds.

No distinct seasonal utilization period is indicated by the identified fauna; all the animals would have been available year-round. A larger sample of culturally incorporated bird remains would be the best indicator for seasonal use, since birds are the most seasonally restricted in terms of breeding activity. Sea mammals can provide indirect seasonal information, however. The presence, possibly, of an immature fur seal innominate suggests a late summer harvest for this individual.

Available data suggest that Goat Island served as a periodic camp site. A broad range of resources was exploited: molluscs, marine fish, sea mammals, and, possibly, sea birds. Individuals probably stayed on the island while resources were collected to conduct initial processing such as butchering, filleting, shucking, and drying. A more permanent settlement is not indicated. While a fresh water spring is present approximately 50 m west of the site, it is fouled by bird waste and unfit to drink.

Island Survey

The presence of the Goat Island site raised the possibility that other offshore rocks and islands were utilized prehistorically, and I therefore undertook a sample survey of offshore rocks and islands administered by the USFWS. The survey area extended from Cape Blanco south to Brookings Harbor, Oregon. Because rocks and islands number in the hundreds and vary with tide heights, I used four criteria to select those to be surveyed. First, the rock or island could not be subject to wave overwash at any time, since it would diminish the probability of artifact retention. This eliminated the majority of rocks from the sample. Second, if the approach was deemed too dangerous due to submerged rocks, lack of disembarking points, or sheer sides, it was not investigated. I assumed that if conditions were similar prehistorically, the rock or island would not have been utilized to any great extent. Third, it had to have vegetation and/or soil development, increasing the odds of any cultural material remaining, since vegetation/soil would indicate limited erosion. Finally, the rock or island could not be connected to land

at extreme low tide. The survey was also constrained by availability of harbor facilities. Only an area extending north from the Chetco River to 48 km north of the Rogue River could be surveyed, given the range of our vessel. Nine rocks were physically inspected (Figure 1). Those without names are designated by a USFWS number. These yielded two additional prehistoric sites, one on Hunters Island (35 CU 173) and one on Whalehead Island (35 CU 174).

Hunters Island is an 8-hectare, steep-sided, vegetated island about 600 m offshore, south of Cape Sebastian (Figure 1). Vegetation obscures the site, which is visible only along a 120 m erosional cut face on the western side of the island. The cultural stratum visible within the cut face has been overlain by a sterile, dark, loamy stratum, and it rests atop a sterile, tan, sandy clay stratum. Artifacts and charcoal are visible throughout this central stratum, but no shell or other faunal remains are visible. Numerous artifacts are scattered across the gradual slope west of the cut face. Most common are oblong river cobbles, averaging 15 cm x 6 cm in size and unifacially flaked along one end to create an acute cutting edge. Steep-end and dome scrapers were also observed. Debitage is rare, and the few pieces noted represent initial reduction stages. Sufficient charcoal was gathered from a lense within the cultural stratum to obtain a radiocarbon date of 1,840 ± 70 B.P. (Beta 33175), falling within the late prehistoric period (Lyman and Ross 1988). No artifacts were collected.

Recorded artifacts suggest heavy butchering tasks and hide processing. However, these tools, which are relatively large and heavy, may owe their presence to their greater resistance to erosion and weathering than lighter, smaller, more specialized tools. Erosion may also account for the lack of visible faunal remains.

Whalehead Island is the outermost of two nearly identical islands located 550 m offshore (Figure 1). Approximately 4.5 hectares in area, the summit of the island is 74 m high. Unlike Goat or Hunters islands, vegetation on Whalehead is restricted to sparse patches of *Scophuleria* and *Calamagrostis*. A broad surface scatter of artifacts extends from the summit of the island down the western slope, covering an area of approximately 60 m^2. The assemblage, nearly identical to that on Hunters Island, consists of cobble choppers, scrapers, and primary flakes. It is unknown whether this assemblage reflects differential erosion or actual extraction and processing tasks. Ongoing erosion makes it doubtful that evidence of human utilization will remain much longer, but the presence of this site in conjunction with the others provides additional evidence of offshore land use and a marine orientation.

Discussion

That direct evidence of prehistoric utilization is not visible on every island surveyed does not discount the possibility that they were important to native groups and utilized for available resources. Erosion, such as that on Whalehead and Hunters islands, may have removed evidence of human activity on other rocks and islands. The coast of southern Oregon is a dynamic environment, subject to winter gales, heavy seas, and driving rains. Soil and vegetative disturbance from animals can accelerate erosional forces. Given these factors, it is remarkable that any offshore rocks retain evidence of human use. Dense vegetation is one of the principal factors preventing erosion, but it may also obscure sites from view. On two easily accessible nearshore islands offering the same broad range of animal resources as the islands with sites, no evidence of human utilization was found, possibly due to dense ground cover. Spruce Island is so thickly covered with salal and spruce, no portion of the ground surface is visible. Although vegetatively similar to Goat and Hunters islands, the ground surface on Saddle Rock is also obscured, necessitating subsurface testing to establish prehistoric use.

The manner in which offshore features were used and the range and nature of activities conducted on them could greatly affect whether or not materials would be left behind to become incorporated into the archaeological record. Collection and harvesting of certain resources may not have required tools, or collecting tools may have been saved for repeated use. Abandoned tools such as collecting baskets, bone fish hooks, nets, or the whalebone clubs used for harvesting sea mammals may have been perishable. Intensity of use would also have affected site development. If occasional, brief forays were made to an offshore feature to collect a few items, cultural deposits would have been less likely to form there, as compared to areas where individuals visited at regular intervals, camped overnight, and processed animals. It is conceivable that only the most intensely utilized island sites were discovered by this survey.

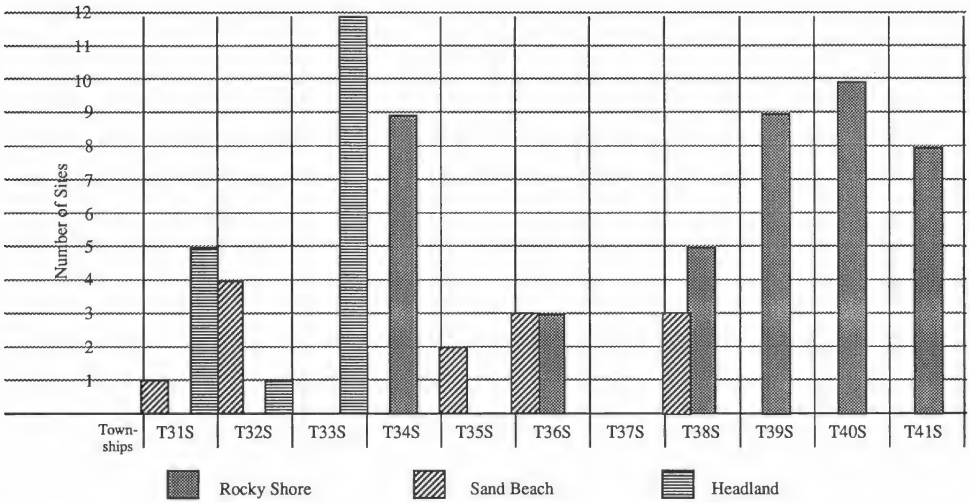

Figure 4. Site frequency by shoreline type, Cape Blanco, Oregon, to the California border.

Site frequencies from Cape Blanco south to California, plotted by township and coastline type (e.g., rocky/sand beach), indicate that higher site frequencies occur along rocky coastal areas (Figure 4). This correlation between rocky shoreline and high site density can be explained by the additional habitat offshore rocks and islands provide, concentrating animal resources in confined, predictable locations.

Conclusion

Draper (1988) found higher settlement density within the marine environment for the southern Oregon coast than had been previously considered, with the majority of coastal sites associated with either stream outlets or bluff/cliff areas. He interpreted this settlement pattern as a site selection strategy based upon proximity to subsistence resources, but he did not support this conclusion with hard data on the type, abundance, or availability of utilized marine resources. I have shown that 1) rocky coastlines are highly productive environments providing a variable, abundant, and year-round food supply of immediate use to humans; 2) this high productivity can be directly related to the increased habitat provided by offshore rocks and islands; and 3) these offshore resources were utilized by prehistoric peoples. Prehistoric use of offshore islands is indicated by data recovered from one tested island site, where intensive use involving the exploitation of a wide range of animals occurred after 900 years ago. Preliminary survey information indicates use of two other island sites, one of which was used approximately 2,000 years ago.

I propose that offshore islands along the southern Oregon coast were valuable foraging areas which played a disproportionate role in the availability of subsistence resources. The high biotic productivity associated with offshore rocks and islands accounts for the correlation between rocky shoreline and site density.

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Beaver Dam Locations and Their Effects on Distribution and Abundance of Coho Salmon Fry in Two Coastal Oregon Streams

Abstract

Beaver (*Castor canadensis*) dams and coho salmon (*Oncorhynchus kisutch*) fry were examined for their relationships in two coastal Oregon streams in 1987. Our initial spring survey of 19 km of stream found only one dam still complete after winter. By autumn, the number of dams had increased to 1.1 and 1.2 per km on the two streams. Beaver dams increased summer pool habitat 7 to 14 percent over unmodified conditions. Although density of coho (per m^2 and m^3) was similar among pool types, beaver ponds were larger and contained more coho fry than non-beaver pools; thus, beaver increased rearing habitat for coho during the late summer low flow. Beaver represent a low-cost tool deserving more consideration for stream rehabilitation projects.

Introduction

Although there is evidence that coho salmon fry use beaver ponds as rearing habitat in the Oregon Cascade Mountains (Everest and Sedell 1983; Everest *et al.* 1985) and in southeastern Alaska (Sanner 1987), beaver generally have been considered detrimental to salmonid populations. Dams have been viewed as barriers to migration and so have been removed (Salyer 1935a,b, Bradt 1947, Patterson 1950, Reid 1952, Marston and Jong 1978, Marston and Deming 1979). Much is known about the general effect of beaver on rivers and streams (Naiman *et al.* 1986), but little reserach has been done in the Northwest, especially in the Oregon Coast Range. The impact of beaver dams on streams and their fish populations may be different in the Coast Range relative to that in the Cascade Mountains or southeastern Alaska because of differences in climate, topography, forest types, and forest management. Most beaver dams in coastal Oregon streams are ephemeral, being washed out in heavy winter storms and rebuilt the next summer (Maser *et al.* 1981). Thus, applicability of existing research on beaver-fish interactions to the Oregon Coast Range is uncertain.

Our objectives in this study were to identify characteristics associated with dam location in two coastal Oregon streams and to assess the effect of stream modification by beaver dams on the rearing habitat of coho salmon.

Study Sites

The two study streams in the central Oregon Coast Range, Cummins Creek and Cape Creek (Figure 1), are underlain by basalt and flow directly into the Pacific Ocean. Both are within the *Picea sitchensis* Zone (Franklin and Dyrness 1973) in which mean minimum temperature in January is 0-2.5°C and mean maximum temperature in July is 20-25°C. The zone receives 200-300 cm of precipitation yearly, most of which falls as rain from October through May.

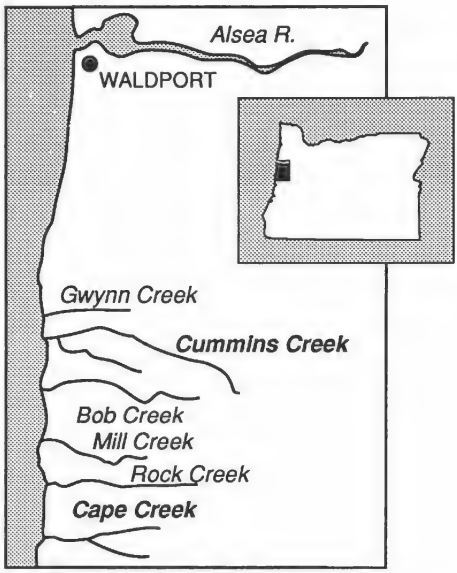

Figure 1. Location of the study sites, main Cape Creek, and Cummins Creek, Oregon.

Cummins Creek

Cummins Creek is a fourth-order 11-km stream draining a watershed encompassing 2,100 ha in

a trellis drainage pattern (the main channel being fed by small tributaries that intersect it at approximately right angles). Average active channel width is the summer is 3 m, and average gradient is 3 percent over the sampled length. The pool:riffle ratio is nearly 4:5; summer discharge near the mouth averages 0.28 m^3/s. The floodplain is wide, 5 to 50 m, and the stream is often braided. Spawning gravel, rearing habitat, and aquatic macroinvertebrate production were judged excellent for juvenile salmonids by Marston and Deming (1979). Gravel bars dominate the channel and are usually associated with large woody debris. There are several log jams, and the upper reaches of the stream are structured with log steps. The basin is moderately stable, although debris slides do occur in undisturbed areas.

Except for the lower 0.4 km, the watershed is managed by the U.S. Forest Service as a wilderness area. Hence, Cummins Creek is in an old-growth watershed except for three small clearcuts (adjacent to a total 350 m of stream) created in 1955, 1963, and 1966-67. Overstory vegetation consists of red alder (*Alnus rubra*), Sitka spruce (*Picea sitchensis*), and Douglas-fir (*Pseudotsuga menziesii*); western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) become more abundant in the upper reaches. Understory vegetation is mainly salal (*Gaultheria shallon*) and salmonberry (*Rubus spectabilis*).

Cape Creek

The main stem of Cape Creek is a fifth-order 15.3-km stream that drains a watershed encompassing 3,292 ha in a dendritic stream pattern, with three major tributaries. The average stream width is 4 m, and the average gradient is 3-4 percent over the sampled length. The pool:riffle ratio is 3:4; summer discharge near the mouth averages 1.3 m^3/s.

More than 70 percent of the watershed has been logged since 1948, generally without maintaining any mature forest buffer strips along streams. In addition, the lower 1.9 km of the main stem was mined for gravel in the late 1950's. The stream has long stretches devoid of large organic debris but is punctuated by large debris jams established by mass wasting from hillside clearcuts and midslope roads or by logging debris. There is little opportunity for a steady addition of large organic debris to the stream as most of the streamside overstory vegetation is young alder that has regenerated after clearcutting. Sitka spruce, western redcedar, Douglas-fir, and western hemlock are also present. The understory is mainly salmonberry and thimbleberry (*Rubus parviflorus*).

Methods

We surveyed the lower 7-8 km of each stream (to the upper limit of coho distribution) for beaver dams and for coho salmon use in April-May and September of 1987. We divided the stream into natural habitat units (reaches) and classified each as pool, riffle, or glide (Hankin and Reeves 1988), then visually estimated their average length, width, and depth. Every tenth unit was measured to provide a correction factor for the visual estimates. Corrections were applied in the mathematical analysis. Definitions of the habitat units, from Bisson *et al.* (1982), are based on occurrences during high water flow as follows:

Pool—an area (including beaver ponds) that is scoured

Riffle—an area of deposition

Glide—an area in which neither deposition nor scouring occurs

Because the volume of the streams decreased substantially from high water in the spring to low water in the fall, a relative measure (percent volume) of the stream in each habitat type was used in comparing results of the spring and fall surveys.

As physical variables generally play an important part in determining dam location (Slough and Sadleir 1977, Howard and Larson 1985, Beier and Barrett 1987) and as they may be important to fish populations, we also examined geomorphology and vegetation. Habitat features potentially important to beaver dam construction were measured along 30-m transects on each side of the stream at each dam site (n = 16) and at sites located at random distances from the stream mouth but more than 100 m from beaver activity. Variables measured were: proximity to log jams, debris slides, and tributaries; bank slope along a 30-m transect perpendicular to each stream; stream gradient; stream width and depth; and cover by woody plant taxa of the understory (less than 2 m tall), midstory (2-10 m tall), and overstory (greater than 10 m tall). Nonparametric discriminant analysis—the k nearest neighbor method, PROC DISCRIM method = NPAR (SAS Institute, Inc., 1987)—was used to identify habitat features that best separated dam sites from random unused sites.

Divers counted coho salmon fry in each habitat unit in the fall by the method described by Hankin and Reeves (1988). Other fish species were not counted. Number of fry per pool and densities were calculated as the sum of the product of habitat-specific densities and habitat frequencies. Student's *t*-test was used to compare the total number of coho fry in beaver and non-beaver pools and the density of fish in pools with the density in glides and riffles.

Results and Discussion

Beaver Dams

In the spring, Cummins Creek had no beaver dams and Cape Creek only one. Casual observation showed that dam construction began in late June, although most construction was done in July and August. We observed new dams being started as late as September. In the fall, we located eight dams (1.2 dams/km) on Cummins Creek and eight (1.1 dams/km) on Cape Creek, low densities in comparison with those found by Naiman *et al.* (1986) in Quebec, Canada (8.6-16.0 dams/km).

The mean sideslope was significantly different ($P \leq 0.05$) on used sites (dams) and unused sites on Cape Creek, the former having a lower slope (10.5%, SD = 2.8 versus 24.8%, SD = 6.7). Slopes of used and unused sites on Cummins were not significantly different, the mean sideslopes being almost identical (9.2% and 8.3%, respectively). The differences may be largely a consequence of the geomorphological difference between the two streams. Nonetheless, the sideslope on used sites was similar on both creeks, approximately 10 degrees. Cummins Creek has a wider flood plain, so neither used nor unused areas are steep.

The tendency of beaver to avoid steep bank slopes has been shown in two other western studies that have examined this variable (Beier and Barrett 1987, McComb *et al.*, 1990) and may be a general western behavior. In contrast, in the Midwest, Urich *et al.* (1983) found that beaver selected steep banks.

Because the sample size was small, the model for discriminant analysis of physical and vegetation variables important to dam location is not presented here. However, the results are at least indicative of relationships and so have some use. Proximity to logjams, tributaries, and debris slides accounted for 52 percent of the model variation, indicating the importance of pre-existing structures to the location of dams. The dams frequently were built on or in front of logjams, or on large wood in the stream channel. Three vegetation variables accounted for an additional 23 percent of the variation. Midstory and overstory conifer cover had a negative association while midstory vine maple (*Acer circinatum*) was positively associated.

The percent volume of streams in non-beaver pools in the spring and fall surveys was fairly constant (Figure 2); however, beaver pools added 7 percent more habitat in Cummins Creek and 14 percent more in Cape Creek—12 percent and 22 percent of the total fall pool volume, respectively. Beaver ponds, on average, were from 3 to 4 times larger than pools formed by other means (Figure 3). Some beaver dams enlarged present pools, often at the expense of riffle or glide habitat. Other dams created pool habitat from riffles or glides.

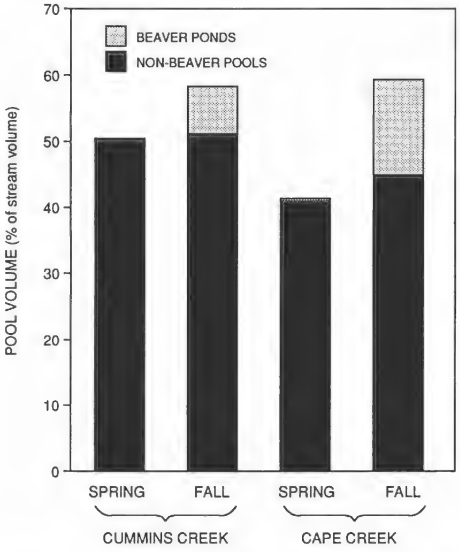

Figure 2. Changes in the percentage of stream volume in pool habitat in Cummins and Cape Creeks, 1987. In the spring survey, no beaver ponds were present at Cummins Creek, and only one small beaver pond at Cape Creek.

Fish-beaver Interactions

The total coho salmon counts of Cape and Cummins Creeks were 8,767 and 3,437, respectively (Table 1). Coho salmon fry were 2 times more abundant in pools than in glides and 40 times more abundant in pools than in riffles, which supports

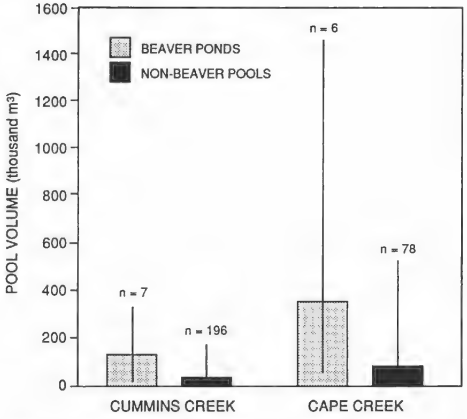

Figure 3. Mean volume and ranges for beaver ponds and non-beaver pools, Cummins and Cape Creek, fall 1987. Number of pools and standard error are shown.

the conclusion that the fry are typically found in pools (Bisson *et al.* 1982, Sedell *et al.* 1984). We also found that coho distribution terminated upstream at a large logjam on Cummins Creek, and that where Cape Creek became very small, beaver dams were not associated with the upstream limit of the coho. The upper limit of coho on Cape Creek appeared to be associated with a continued diminution of stream width and an increase in stream gradient.

The mean number of coho fry in beaver ponds was three times the mean number in non-beaver pools, although the variance was too high to be statistically significant (Table 2). Density of coho fry by area and volume did not differ in beaver ponds and non-beaver pools; thus, it appears that the fry use the habitat created by beaver in these streams. We have no evidence that fry were actively selecting beaver ponds; rather, they were using large pools, and beaver ponds tended to be larger than non-beaver pools.

The presence of beaver in these two coastal Oregon streams seemed to affect coho populations positively by increasing the availability of pools, the preferred coho habitat (Bisson *et al.* 1988). We did not observe the decreases in density that have been reported in the midwestern United States for fish species of that region (Salyer 1935a,b, Patterson 1950, Reid 1952). The coastal streams are steeper, faster, and generally colder in summer than midwestern streams, where large temperature rises and low levels of dissolved oxygen are associated with beaver dams in the low-gradient stream systems. In this coastal environment, the moderate slowing and deepening of

TABLE 1. Total stream length, area and volume in the habitat units, and average coho salmon density in each unit. N is the number of units sampled in fall 1987.

Stream habitat unit	N	Length (m)	Area (m^2)	Volume (m^3)	Average fish density	
					m^{-2}	m^{-3}
Cape Creek						
Pool	22	2,307	19,210	8,935	0.554	1.500
Glide	12	2,898	21,321	3,965	0.080	0.387
Riffle	10	3,050	22,527	2,478	0.014	0.143
Cummins Creek						
Pool	42	3,741	22,518	7,430	0.107	0.332
Glide	18	2,322	13,341	2,601	0.036	0.156
Riffle	30	4,856	23,310	2,833	0.000	0.000

TABLE 2. Comparison of coho fry populations in beaver and non-beaver pools, by pool, density per area, and density per volume. Values are for Cape Creek and Cummins Creek combined, fall 1987. Student's *t*-test was used to compare population sizes.

Population	Beaver ponds (n = 14)		Non-beaver pools (n = 45)		
	Average	(SD)	Average	(SD)	*P*
Coho/pool	108.43	(179.68)	35.62	(56.76)	0.16
Coho/m^2	0.34	(0.38)	0.26	(0.38)	0.49
Coho/m^3	0.95	(0.75)	0.71	(1.02)	0.43

streams by beaver dams improves the quality of summer habitat by increasing the amount of slow water in pools (Bisson *et al.* 1988). Beaver ponds raise the level of a stream and may also provide access to side channels as the water level decreases, therefore preventing fry from becoming stranded in side-channel ponds.

Our spring survey showed that most dams were destroyed by winter high water; however, they were not always washed entirely away. Remnant ends of dams along banks may provide some slow-water refuge (sensu Sedell *et al.* 1990) during high water events. The side channels, canals, and dams developed at a beaver site also could be important winter habitat for coho fry. Careful study of stream energetics is needed to evaluate if beaver-caused changes in the stream system result in changes in fish productivity or changes in the composition of the fish community.

An important question to ask, but for which answers can only be speculative, is why there are so many more coho salmon in Cape Creek than in Cummins Creek. The streams differ in both small and large ways; any or all of which may contribute to the difference in coho population size. A very significant difference between the streams is their management history, which suggests testable hypotheses on the interactions between coho populations and streamside community structure and disturbance. Off-shore harvest of salmon may also have affected within-stream populations.

Management Implications

Stream enhancement projects instituted in some anadromous fish streams in the Pacific Northwest (Bisson *et al.* 1987) have demonstrated that structures can increase spawning or rearing habitat (Everest and Sedell 1983), but they have also shown that stream enhancement can be expensive (Bisson *et al.* 1987). Costs for placing an individual boulder ranged from $22 to $35. The estimated average cost for an individual gabion was $1200. Installation of gabions to retain spawning gravel in tributaries of the Coos River in Oregon cost $225,000 in 1981, excluding costs of engineering design and roads (Bisson *et al.* 1987). These projects may be more costly than foregoing timber harvest to allow beaver and riparian trees to contribute to stream structure (House and Crispin 1990).

On banks of low-gradient coastal streams that have been extensively harvested and cleaned, beaver offer an alternative to engineered improvements aimed at increasing coho-rearing habitat. While beaver dams are not structurally the same as other accumulations of large woody debris, they can provide some of the same benefits: increased pool area in the stream, slower water, increased productivity in pools (Naiman *et al.* 1986, 1988), and refuge during high water. Hence, maintaining high beaver densities in coastal streams is an additional tool to be considered in the development of management strategies for coho salmon production.

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Non-salmonid Fishes and Morphoedaphic Features Affect Abundance of Trouts in Wyoming Reservoirs

Abstract

Quantitative relations between the abundance of trout in reservoirs and chemical, physical, and biological factors are not well defined. We assessed standing stocks of trout in 22 reservoirs in Wyoming for their relation to the abundance of non-salmonid fishes and morphoedaphic features. Trout standing stocks were lower in reservoirs where non-salmonid fishes were abundant, but increased as total dissolved solids increased. A two-variable (non-salmonid fishes and total dissolved solids) multiple-regression model accounted for most variation ($R^2 = 0.56$) in trout standing stocks. Our results suggest the possibility of competition between trout and non-salmonid fishes in Wyoming reservoirs. They also indicate that total dissolved solids influence biological productivity and trout abundance in an asymptotic manner at concentrations between 54 and 14,442 mg/L.

Introduction

Factors governing the abundance of trout in reservoirs are poorly understood. We examined the standing stock of trout in small ($\leq$890 surface hectares at full pool) reservoirs in Wyoming relative to the abundance of non-salmonid fishes that may compete for food or space and to chemical and physical features that have been related to fishery production in lakes. Quantitative relations among such variables can be useful in explaining their biological significance to trout and in managing impoundments of the Rocky Mountains for sport fisheries.

Non-salmonid fishes and trout in lakes or reservoirs can utilize similar food resources (Schneidervin and Hubert 1987). Evidence of possible competition for food resources between trout and non-salmonid fishes has been found in some lakes (Purych 1977, Fraser 1978, Barton and Bidgood 1980), but not in reservoirs (Marrin and Erman 1982). Johannes and Larkin (1961) demonstrated competition for food resources between a minnow and trout in a natural lake in British Columbia, but they emphasized that the observation could have been easily missed without comprehensive field work.

Several physical and chemical features influence fishery production (Rawson 1952, Murphy 1962, Hayes and Anthony 1964, Jenkins 1970). The best known is the morphoedaphic index (MEI) which has been shown to be related to fishery production in numerous lakes (Ryder 1965, 1982). The MEI is computed as total dissolved solids (TDS) divided by mean depth of the lake.

Whitworth (1985) examined the relation of 24 physical, chemical, and biological parameters to trout abundance in small Wyoming reservoirs. He found the two best predictors of trout standing stock were maximum water depth at full pool and TDS, variables similar to those in the MEI. However, Whitworth did not evaluate the possible influence of non-salmonid fishes on trout abundance.

Guenther (1989) used 11 reservoirs sampled by Whitworth (1985) and 12 reservoirs that she sampled in Wyoming to assess factors influencing trout abundance. She found TDS, surface area, and MEI to be negatively correlated with trout standing stocks, while mean depth was positively correlated. Negative correlations for TDS and MEI seemed to have been due to the abundance of non-salmonid fishes in several reservoirs. When nine reservoirs with $<20\%$ of the total fish biomass composed of non-salmonid fishes were assessed, a positive correlation between trout standing stocks and both TDS and MEI were found.

We know of no previous work on the interaction of the abundance of non-salmonid fishes and morphoedaphic features with standing stocks of trout in reservoirs. We hypothesize that the abundance of non-salmonid fishes reduces trout abundance, whereas certain chemical or physical features of reservoirs favor trout abundance.

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[2]The Unit is jointly supported by the University of Wyoming, the Wyoming Game and Fish Department, and the U.S. Fish and Wildlife Service.

Methods

We studied 22 reservoirs in Wyoming that were ≤890 hectares surface area at full pool, 1253-3166 m above mean sea level, and constructed to store water for irrigation or municipal use. Spring runoff from melting mountain snow fills the reservoirs and they are drawn down during the remainder of the year. All of the reservoirs feature angling for trout. The Wyoming Game and Fish Department or private interests stock the reservoirs with various combinations of fingerling rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*), brown trout (*Salmo trutta*), and brook trout (*Salvelinus fontinalis*). Naturally reproducing populations of non-salmonid fishes, notably white suckers (*Catostomus commersoni*), longnose suckers (*Catostomus catostomus*), and yellow perch (*Perca flavescens*), were present in many of the reservoirs.

Mark and recapture techniques were used to estimate the abundance of trout in each reservoir during summer. Between 1981 and 1984, Whitworth (1985) sampled fish in 10 reservoirs of 50-890 hectares with trap nets (25-mm square mesh) and a 9 x 183 m purse seine (9-mm mesh). Trap nets were set at randomly assigned locations with leads extending perpendicular to the reservoir bank for approximately 24-h periods. Purse seining locations were randomly assigned from a grid system mapped for each reservoir. All captured trout were weighed, fin-clipped and then released near the point of capture during the initial capture period. A two-sample Schnabel estimator was used to estimate the number of the trout in the reservoir (Ricker 1975). Computations were made with Model Mo of program CAPTURE (White *et al.* 1983). All non-salmonid fishes were identified and enumerated. Two reservoirs sampled by Whitworth (1985) were omitted because the trout sampling techniques differed from the 10 reservoirs described here.

In 1987 and 1988, we sampled the fish in 12 reservoirs of 3-49 hectares with 8-9 trap nets (25-mm mesh) located around the periphery of each reservoir (Guenther 1989). All captured trout were weighed and marked with a caudal fin punch. A multiple-census Schnabel estimator was used with up to 10 mark and recapture episodes within a 2-week period to estimate the number of trout (Ricker 1975). All non-salmonid fish were identified and counted.

Trout standing stocks were computed for each species from the estimated number of trout in the reservoir multiplied by the mean weight of fish in the sample divided by the surface area of the reservoir. The proportion of non-salmonid fishes was computed from the number of non-salmonid fishes and trout captured in each reservoir.

Total dissolved solids (TDS) were determined gravimetrically from water samples taken at the time of fish sampling (APHA 1985). Mean water depth, maximum water depth, and surface area were measured from bathymetric maps at full pool. The morphoedaphic index (TDS/mean depth) was computed for each reservoir.

Statistix 3.1 (Analytical Software 1990) was used for correlation and multiple-regression analyses. The Wilk-Shapiro/Rankit Plots procedure was used to determine normality of individual variables. The distributions of all chemical and physical variables were transformed ($\log_{10}$) to normalize the distributions. Significance was determined at $P \leq 0.05$ for all procedures.

Results

The standing stocks of trout ranged from 0.2 to 139.2 kg/hectare among the 22 reservoirs (Table 1). Among the dependent variables, only the proportion of non-salmonid fishes was significantly correlated ($r = -0.61$) with trout standing stock. Multiple-regression analysis yielded only one two-variable model with both independent variables that were significant. Variation in standing stocks of trout was accounted for by the proportion of non-salmonid fishes and TDS ($R^2 = 0.56$):

$$SS = -4.3 - 9.498\ NS + 23.5\ \log_{10}TDS$$

where, SS is the standing stock of trout (kg/hectare), NS is the percentage of the total fish stock composed of non-salmonid fishes, and TDS is the total dissolved solids concentration (mg/L). Figure 1 illustrates the relationship between trout standing stock and TDS at three levels of abundance of non-salmonid fishes based on the multiple-regression model.

Discussion

The abundance of non-salmonid fishes and an index of biological productivity (TDS) accounted for variability in standing stocks of trout in small Wyoming reservoirs. The abundance of non-salmonid fishes was negatively related to trout abundance. However, our data are limited because 9 of 22

TABLE 1. Standing stocks of trout, relative proportion of non-salmonid fishes, and physical features of 22 small reservoirs in Wyoming, 1981-1988.

Reservoir	Standing stock of trout (kg/ha)	Proportion non-salmonid fishes (%)	Total dissolved solids (mg/L)	Mean depth (m)	Maximum depth (m)	Surface area (ha)
Twin Buttes	139	20.0	14442	3.7	9.2	135
Soda Lake, Fremont County	101	1.6	3391	7.3	13.4	120
Diamond	88	0	3964	1.8	9.1	102
East Lake	76	0	253	2.8	6.6	25
Greyhound	51	1.4	379	2.7	3.9	12
Cameahwait	51	89.3	364	4.9	11.3	168
Shirley Basin	48	0	2457	3.1	4.5	6
Kemmerer City	44	96.1	237	1.2	7.6	51
Harney	35	0	196	5.8	8.8	3
Miller	30	0	110	2.2	3.3	6
Chapman	29	0	54	4.4	6.6	8
Mortenson	20	76.9	646	1.8	3.0	29
Healy	10	96.8	479	11.5	29.6	600
LAK	9	93.6	1910	5.2	15.2	50
Sucker Lakes	6	0	84	1.2	2.6	5
Viva Naughton	5	97.4	940	11.3	37.2	890
Lower Sunshine	4	98.7	189	20.2	55.5	497
Upper Sunshine	3	98.0	158	14.0	36.6	469
Leazenby	2	99.3	273	0.6	1.6	13
Sand Lake	2	96.5	71	2.6	5.0	37
Nine Mile Lake	1	98.3	10112	2.2	3.7	49
Soda Lake, Albany County	<1	99.9	5246	3.2	4.4	26

reservoirs had ≤ 1.6 percent non-salmonid fishes and 11 had ≥ 89.3 percent non-salmonid fishes.

Use of the same food resources by non-salmonid fishes and trout has been shown to occur in reservoirs (Schneidervin and Hubert 1987), but competition for food resources has not been demonstrated. For example, Marrin and Erman (1982) found no evidence of competition between non-salmonid fishes and trout in a California reservoir. However, Gipson and Hubert (1991) found a negative relation between the body condition of rainbow trout and the abundance of non-salmonid fishes among 13 reservoirs in Wyoming.

Among natural lakes in Canada, evidence of competition between non-salmonid fishes and trout has been observed. Johannes and Larkin (1961) reported competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout in a British Columbian lake. Purych (1977) observed potential competition between non-salmonid fishes and native salmonids in an Ontario lake. A negative influence of white suckers and longnose suckers on growth of rainbow trout was suggested by Barton and Bidgood (1980) in an Alberta lake. Fraser (1978) provided evidence that yellow perch reduced the growth and survival of trout in an Ontario lake. Similarly, we observed a negative relation between the abundance of non-salmonid fishes and standing stocks of trout among Wyoming reservoirs, but the mechanism causing this relation was not defined.

Higher concentrations of TDS favored trout abundance. Fishery production has been related to TDS in other lakes and reservoirs (Jenkins 1968, 1982, Ryder 1982). The relation between TDS and trout standing stocks in Wyoming reservoirs is a function of not only biological productivity, but also stocking rates of fingerling trout. Experience

has taught managers which reservoirs are more productive, and these reservoirs subsequently have been stocked with larger numbers of trout fingerlings to increase the standing stocks.

The asymptotic relation between trout abundance and TDS in Wyoming reservoirs (Figure 1) is possibly a function of very high TDS (>10,000 mg/L) in two of the reservoirs studied (Table 1). Trout production in saline waters can be limited by either physiological or toxic effects of dissolved salts. Rainbow trout generally tolerate up to 7,000 mg/L TDS, but beyond this level survival, growth, and food conversion efficiency are reduced (Piper *et al.* 1982). It is also possible that these two reservoirs have been stocked with fewer fish than the reservoirs may be able to support.

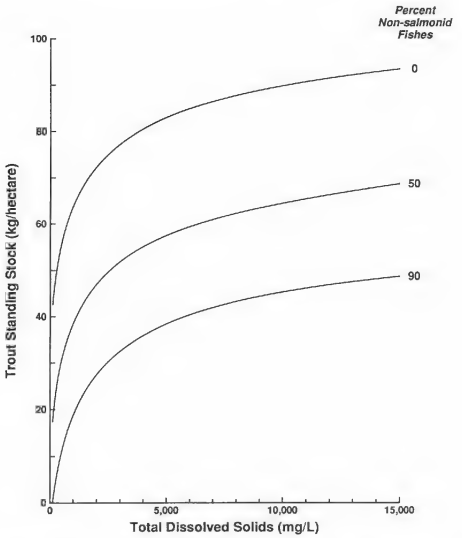

Figure 1. The relationships between trout standing stocks and total dissolved solids in Wyoming reservoirs at three levels of abundance of non-salmonid fishes.

The extent to which reservoirs are drawn down is also likely to affect the abundance of trout. The timing and magnitude of draw-down affect reservoir productivity, spawning success of fishes, and predator-prey interactions (Ploskey 1983). Among the reservoirs that we studied, water levels fluctuated from less than 1 m to more than 15 m annually. The extent to which water level fluctuations affected trout abundance in the reservoirs that we studied is unknown.

Our observations suggest that competition may occur between non-salmonid fishes and trout in Wyoming reservoirs. They also indicate that higher TDS concentrations, an index of biological productivity, enhance standing stocks of trout in reservoirs, but the effect may be less at very high levels of salinity (>10,000 mg/L). The relations should be further evaluated because of the small sample size and limited geographic area of this study, but our results provide a base for future work.

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Quantifying Vegetation Response to Recreational Disturbance in the North Cascades, Washington

Abstract

The purpose of this study was to (1) describe vegetational response to various levels of controlled recreational trampling and (2) explore variation in response between different vegetation types and species. Better information on the ability of vegetation to resist and recover from damage is needed by park and wilderness managers to minimize impacts caused by recreationists. Four vegetation types were trampled at intensities that ranged from 25 to 700 times. Responses shortly after trampling and after one year of recovery were documented. Vegetational response varied significantly both with trampling intensity and between vegetation types. A sedge meadow dominated by black alpine sedge was about 25 times more resistant to trampling damage than a subalpine forb meadow, in which Sitka valerian was the most abundant species. Recovery during the year that followed trampling was greatest in the forb meadow; it was lowest in the two vegetation types dominated by woody species—heather and mountain boxwood. The resistance and resilience of individual species was also assessed. Species resistance appears to be determined primarily by the stature, arrangement, and toughness/flexibility of aerial tissues. Resilience appears to be determined by the location and toughness of perennating tissues and by the growth rate of regenerating tissues. These results have immediate application to recreation managers and also increase our basic understanding of disturbance ecology.

Introduction

The nature of disturbance in natural communities has generated considerable interest among ecologists (Souza 1984). Much basic research has been conducted on vegetational responses to natural disturbance agents such as fire, wind, landslides, and volcanic eruptions (White 1979). Applied ecologists have complemented this work with studies of human-caused disturbances, from relatively localized disturbances such as oil spills (Hutchinson and Freedman 1978) and the construction of winter seismic trails (Felix and Raynolds 1989), to more widespread disturbances such as livestock grazing and logging (Vale 1982).

One disturbance agent that has become increasingly important in recent decades is the recreationist. Substantial quantities of land have been set aside as national parks and wilderness for the purpose of nature preservation. Such places are also available for recreational use, however, and recreational use of these wildlands has increased dramatically. This use commonly compromises preservation goals. One of the most serious types of recreational impact is damage to vegetation caused by trampling at campsites and along trails. Park and wilderness managers often seek to control such impacts by restricting amount of use or by attempting to channel use onto the vegetation types that are most durable. To do this effectively, managers need information about vegetation response to different levels of trampling stress, as well as about the relative durability of different vegetation types.

The objective of this paper is to describe the effects of recreational trampling on vegetation in the northern Cascade Mountains of Washington. Specifically, it reports the results of experiments in which carefully controlled levels of trampling are applied to vegetation plots. Several experimental trampling studies have already been conducted in the mountains of western Washington. Bell and Bliss (1973) and Schreiner (1974) studied the initial trampling responses of alpine and subalpine meadow communities in the Olympic Mountains. Singer (1971) studied the trampling response of an alpine community on Mt. Rainier. This paper extends this research by describing the results of trampling experiments in four vegetation types from the northeastern Cascade Mountains. Compared with earlier work, this study examined a broader range of vegetation types, from montane forest to alpine meadow, and included both initial damage and subsequent recovery.

Methods

Study Sites

The four study sites were located on the Okanogan National Forest, along the crest and east slope

of the Cascade Mountains. One site (denoted by the generic name of the most abundant understory plant, *Pachistima*) was located at an elevation of about 760 m along the upper Methow River. It was characterized by a moderately dense tree canopy (50-75% cover) entirely of Douglas-fir (*Pseudotsuga menziesii*), with a relatively sparse understory entirely of Douglas-fir. Associated groundcover plants were only moderately dense and consist primarily of shrubs, particularly mountain boxwood (*Pachistima myrsinites*) (Table 1). Nomenclature follows Hitchcock and Cronquist (1973).

Two of the other vegetation types occurred intermixed with each other in a mosaic of subalpine forest and meadow near Harts Pass; elevation was about 1750 m. Both had an overstory of subalpine fir (*Abies lasiocarpa*), with a smaller number of large Engelmann spruce (*Picea engelmannii*). The groundcover of one type (*Phyllodoce*) was dominated by a dense cover of low shrubs, particularly heather (*Phyllodoce empetriformis*) and huckleberry (*Vaccinium membranaceum*). The other type (*Valeriana*) was characterized by a dense cover of tall broad-leaved herbs, of which valerian (*Valeriana sitchensis*) was most abundant. These groundcovers occurred both under and away from the forest canopy. Most of the experimental units were in small openings, but adjacent to forest.

The final type (*Carex*) was a sedge meadow, located on the slopes of Slate Peak at an elevation of about 2000 m. The sites were located in swales where snowmelt is unusually late; the dominant species was black alpine sedge (*Carex nigricans*).

TABLE 1. Initial frequency and mean percent cover of the more abundant species in each of the four vegetation types.[1]

	Vegetation type							
	Pachistima		*Phyllodoce*		*Valeriana*		*Carex*	
Species	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover
Pachistima myrsinites	98	46						
Amelanchier alnifolia	70	9						
Phyllodoce empetriformis			100	81				
Vaccinium membranaceum			93	15				
mosses	13	+	58	7	74	20	73	9
Ligusticum grayi			38	3	28	6		
Valeriana sitchensis			25	2	96	40		
Lupinus latifolius			18	2	13	3		
Arnica mollis			23	2				
Potentilla flabellifolia			28	2	48	8	45	7
Aster alpigenus			25	2	43	6		
Erigeron peregrinus			35	2	18	2		
Trollius laxus			8	1	58	19		
Mitella breweri					67	16		
Senecio triangularis					57	12		
Thalictrum occidentalis					41	11		
Carex spectabilis			8	+	25	5	28	5
Heracleum lanatum					18	5		
Equisetum palustre			3	+	35	5		
Osmorhiza purpurea					26	5		
Luzula hitchcockii					22	5	8	1
Veratrum viride					7	2		
Phleum alpinum			5	+	16	2		
Carex nigricans							100	87
Juncus drummondii							43	9
Veronica cusickii					1	+	55	6
Hieracium gracile							45	4

[1]Only species with mean cover of at least 2% are included. Frequency is the percent of the forty 30 X 50-cm subplots in which the species was found. A + indicates cover <0.5%.

Field Methods

Four replicate sets of experimental trampling lanes were established in each vegetation type. Each set consisted of five lanes, each 0.5 m wide and 1.5 m long. Where the lanes occurred on a slope, they were oriented parallel to contours. Treatments were randomly assigned to lanes. One lane was a control and received no trampling. The other lanes received either 25, 75, 200, or 500 passes in three of the four vegetation types. In the fourth type (*Carex*), which was highly resistant to impact, treatments were 75, 200, 500, and 700 passes. A pass was a one-way walk, at a natural gait, along the lane. The weight of the tramplers was about 70 kg and tramplers wore lug-soled boots.

Measurements were taken on each lane in two adjacent 30 X 50-cm subplots. In each subplot. the cover of each vascular plant species, and of lichens and mosses, was estimated. Trampling treatments were administered in July 1988. Initial measurements were taken immediately before trampling. Followup measurements were taken about two weeks after trampling occurred and again one year after trampling.

Data Analysis

The primary response variable for each vegetation type was relative vegetation cover, a measure of the proportion of original vegetation that survives trampling, adjusted for changes on controls. It was calculated by (1) summing the covers of all individual species to obtain total cover and then (2) calculating relative vegetation cover as:

$$\frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots}} \times \text{cf} \times 100\%,$$

$$\text{where cf} = \frac{\text{initial cover on control subplots}}{\text{surviving cover on control subplots}}$$

Relative vegetation cover after trampling and after one year of recovery was calculated for each trampling treatment.

For the most widespread individual species it was also possible to calculate relative cover. For most species, however, it was only possible to discuss their response in qualitative terms.

Results and Discussion

Response of Vegetation Types

The immediate response of vegetation cover to trampling differed significantly both with amount of trampling and with vegetation type (analysis of variance, $p < 0.001$). The interaction between these two main effects was also significant, but the magnitude of this interaction effect was negligible compared with the main effects.

The relationship between relative vegetation cover and amount of trampling for the four vegetation types is illustrated in Figure 1. Mean relative vegetation cover and standard errors are given for measurements after trampling and after one year of recovery. With only one exception, vegetation cover declined with each successive increase in number of passes. In the *Carex* type, no vegetation cover was lost until the trampling intensity reached 200 passes. With the exception of the *Valeriana* type, the relationship between relative cover and amount of trampling was generally linear. In the *Valeriana* type, substantial vegetation was lost at low levels of trampling, but additional increments of trampling caused successively less damage. This curvilinear relationship is more similar to that reported elsewhere (Cole 1985).

The most resistant vegetation type was clearly the *Carex* type. Seventy-five passes resulted in no cover loss and, even on the 200-pass lane, only a trained observer would have noticed the trampling impact. Relative cover was still 62 percent after 500 passes. The *Pachistima* type was also quite resistant. Cover loss occurred more rapidly than in the *Carex* type, although the difference between the types was not statistically significant. Relative cover on this type was 81 percent after 75 passes and 55 percent after 500 passes. Of more importance, however, was the fact that damage was much more apparent in the *Pachistima* type. Broken branches and stripped leaves on shrubs were apparent after just 75 passes, and a path was readily apparent after 200 passes.

The other two vegetation types were significantly less resistant. The *Phyllodoce* type had a relative cover of 67 percent after 75 passes and only 6 percent after 500 passes. An obvious path had developed after only 75 passes. The *Valeriana* type was significantly more fragile than even the *Phyllodoce* type. Relative cover was reduced by more than 50 percent after just 25 passes; 500 passes eliminated all but a few plants (2% relative cover). An obvious path had developed after just 25 passes and, after 75 passes, all upright stems had been eliminated.

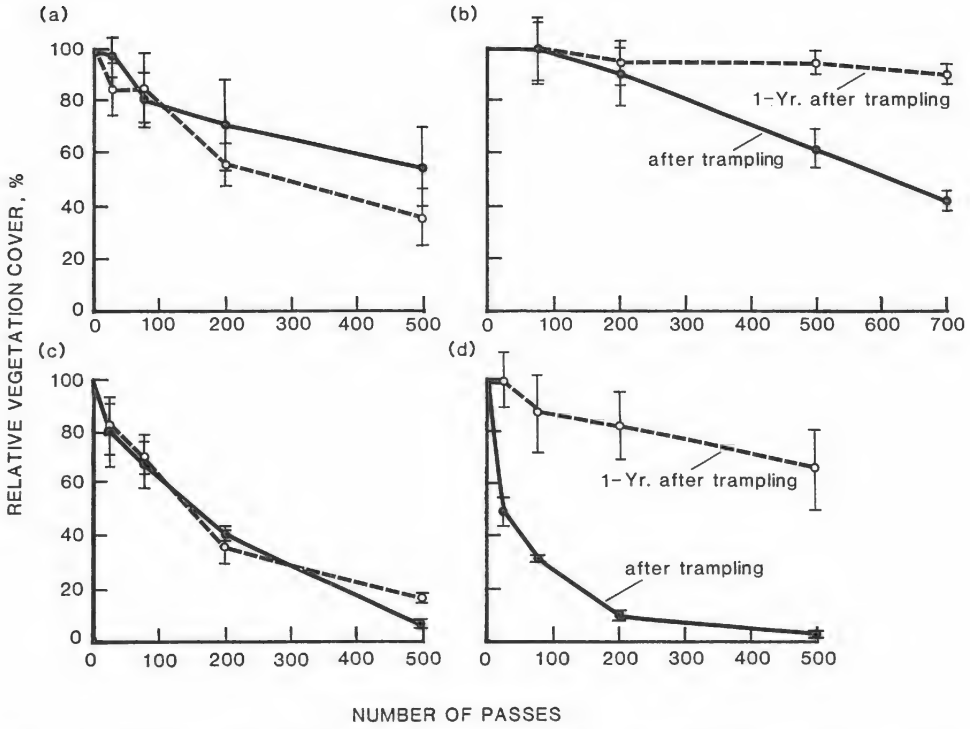

Figure 1. The relationship between vegetation cover and amount of trampling in the (A) *Pachistima*, (B) *Carex*, (C) *Phyllodoce*, and (D) *Valeriana* vegetation types. Bars are one standard error.

Differences between vegetation types and trampling treatments declined somewhat in the year following trampling; however, both main effects—vegetation type and amount of trampling—were highly significant ($p < 0.001$). The interaction between the two was not.

One year after trampling, disturbance was difficult to detect on all but the most heavily trampled lanes in both the *Carex* and *Valeriana* types. Both of these types recovered substantially during the year after trampling was curtailed. In the *Carex* type, relative cover was 62 percent after 500 trampling passes; one year later, relative cover had increased to 95 percent. In the case of the *Valeriana* type, the amount of recovery that occurred over the year was even more dramatic. Relative cover increased from two percent after 500 passes, to 66 percent one year later. These two types, which differed most in their initial response to trampling, were not significantly different after one year of recovery.

The *Phyllodoce* and *Pachistima* types remained significantly more damaged than the other types after the year of recovery. In each of these types, the 75-pass lane remained obviously damaged even after a year without disturbance. The relative cover of these two types was not significantly different, but their response over the year of recovery was different. The *Phyllodoce* type, which had been more substantially damaged initially, remained relatively unchanged over the year of recovery. Only the lane trampled 500 times experienced an increase in cover of more than five percent. On this type it was primarily forbs that recovered—not *Phyllodoce empetriformis*. Cover on the *Pachistima* type actually declined. Many shrub branches survived trampling damage for a short time, but died during the following winter. Relative

cover after 500 passes was 55%, but after one year of "recovery," cover had declined to just 36%.

The durability of any vegetation type is a reflection of both its ability to resist being disturbed by trampling and its ability to recover from trampling disturbance. The terminology used when describing these two properties is confusing. We follow Cole (1988), Kelly and Harwell (1990), and Sun and Liddle (1991) in using the term *resistance* when referring to the ability of an ecosystem to resist change when subjected to disturbance. This property has also been called inertia by Orians (1975), Cairns and Dickson (1977), Westman (1978) and Grime (1979). Resistance to trampling was assessed with data on immediate responses to trampling. We follow Westman (1978), Grime (1979), Cole (1988), and Kelly and Harwell (1990) in using the term *resilience* when referring to the ability of an ecosystem to recover rapidly following disturbance. Resilience was assessed by comparing relative vegetation cover immediately after trampling with cover after one year of recovery. This property is similar to that defined as elasticity by Orians (1975) and Westman (1978) and as recovery by Sun and Liddle (1991).

We also find it useful to characterize the ability of a vegetation type to both resist and recover from trampling—a property that we term *tolerance*. Tolerance was assessed by comparing vegetation cover after one year of recovery from trampling with cover prior to the trampling treatments. A measure of tolerance provides a single overall indication of durability, but it does not indicate, for example, whether a high level of tolerance results from an ability to resist damage, an ability to recover from damage, or both.

The four vegetation types vary greatly in all three of these properties. At one extreme is the *Carex* type, which is highly resistant, resilient, and tolerant. The *Valeriana* type exhibits low resistance but high resilience; consequently, tolerance is also relatively high. The *Pachistima* and *Phyllodoce* types are moderately resistant, but not at all resilient; consequently, their tolerance is low.

Response of Individual Species

It was possible to calculate relative cover for nine vascular species and for mosses, as a group. The other species were too sparse or irregularly distributed to provide meaningful results. The responses of individual species to trampling are more diverse than the response of entire assemblages of species (Table 2). A plot of initial response to light trampling (25 passes) on one axis and response to heavy trampling (500 passes) on the other axis reveals three general types of response (Figure 2). *Carex nigricans* and *Pachistima myrsinites* are generally resistant to trampling. Four species—*Trollius laxus, Valeriana sitchensis, Potentilla flabellifolia,* and *Mitella breweri*—are generally susceptible to trampling disturbance. The others—*Senecio triangularis, Vaccinium membranaceum, Phyllodoce empetriformis,* and mosses—resist light trampling but are susceptible to heavy trampling.

In a similar plot of cover after the year of recovery (Figure 3), groupings are less discrete. At one

TABLE 2. Relative cover[1] of abundant species after trampling and after one year recovery.

	After trampling					After one year recovery				
	Number of passes					Number of passes				
Species	25	75	200	500	700	25	75	200	500	700
Carex nigricans	–	96	96	78	53	–	106	104	104	95
mosses	95	100	37	12	–	143	136	135	108	–
Pachistima myrsinites	89	71	68	62	–	68	68	43	22	–
Phyllodoce empetriformis	99	90	54	11	–	90	71	26	7	–
Vaccinium membranaceum	93	54	6	0	–	69	46	44	40	–
Mitella breweri	67	50	20	1	–	116	113	99	60	–
Potentilla flabellifolia	58	31	15	16	–	86	86	75	79	–
Senecio triangularis	86	36	1	0	–	119	115	59	65	–
Trollius laxus	43	37	11	5	–	74	69	55	73	–
Valeriana sitchensis	58	26	5	2	–	102	74	69	70	–

[1]Relative cover is the proportion of original cover that survives trampling, adjusted for changes on controls.

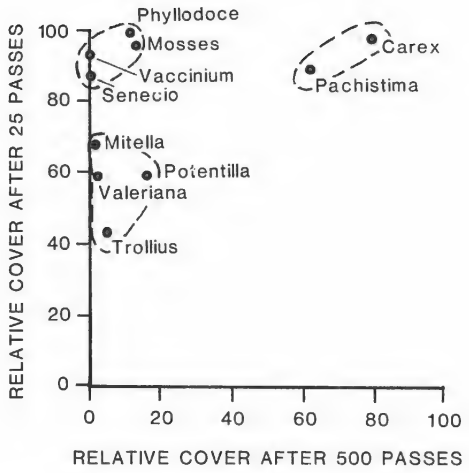

Figure 2. Mean relative cover of abundant species after light and heavy trampling.

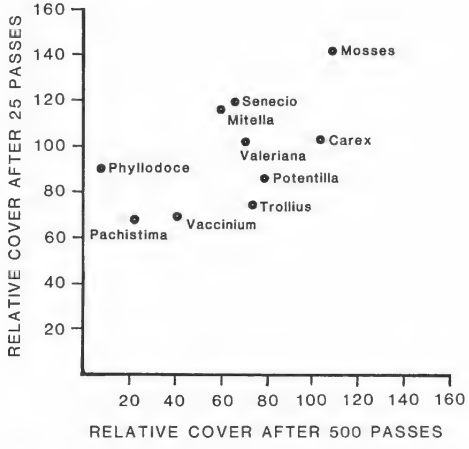

Figure 3. Mean relative cover of abundant species after one year of recovery following light and heavy trampling.

extreme are the highly tolerant mosses and *Carex nigricans*. Following one year of recovery, relative cover exceeds 100 percent, regardless of how heavily they were trampled. At the other extreme are the three shrub species, which have relative cover values of less than 100 percent at all levels of trampling, and cover values of 40 percent or less on the lanes trampled 500 times.

In an effort to assess the resistance and tolerance of less common species, we prepared tables of mean cover before trampling, immediately after trampling, and one year after trampling, for each level of trampling intensity. From these tables it was possible to identify the trampling levels that clearly caused substantial cover loss. We used these data to develop a simple classification of the resistance and tolerance of less common species. Species were considered resistant if more than 50 percent cover survived after 75 passes. Species were considered tolerant if cover exceeded about 75 percent of original cover one year after trampling on lanes trampled at least 200 times.

Four groups of species can be identified. Species that were both resistant and tolerant included *Antennaria lanata, Carex nigricans, Carex spectabilis, Hieracium gracile, Juncus drummondii, Leptarrhena pyrolifolia, Luzula hitchcockii, Veronica cusickii, Viola orbiculata,* and mosses. These are all low growing plants that have either a tufted growth form or leaves in basal whorls that grow flat against the ground. All of the graminoids species fall into this category. A smaller group of species were resistant but intolerant: *Pachistima myrsinites, Phyllodoce empetriformis, Vaccinium membranaceum,* and *Vaccinium scoparium.* These four woody shrub species lack resilience, so they are unable to tolerate even moderate levels of trampling.

The largest group of species were nonresistant but tolerant: *Arnica mollis, Equisetum palustre, Heracleum lanatum, Ligusticum grayi, Lupinus latifolius, Mitella breweri, Saxifraga arguta, Senecio triangularis, Thalictrum occidentale, Trollius laxus, Valeriana sitchensis,* and *Veratrum viride.* These were all broad-leaved herbaceous plants with upright stems. This growth form has little capacity to resist trampling damage, but these species are able to regenerate rapidly from subsurface adventitious buds that escape damage.

The final group are species that are both nonresistant and intolerant: *Abies lasiocarpa* seedlings, *Caltha bicolor, Gentiana calycosa, Osmorhiza purpurea, Parnassia fimbriata, Pedicularis bracteosa,* and *Viola glabella.* The tree seedlings were somewhat resistant to low levels of trampling. Once they were damaged, however, they usually died and their loss was not offset by establishment of new seedlings. The other species—all broad-leaved herbs—are all relatively uncommon species that were highly fragile. Their aerial parts were generally entirely eliminated after as few as 25 passes. Apparently their regenerative tissues were damaged as well, making recovery from damage slow.

Three broad-leaved herbaceous species were unique in that their response varied between vegetation types. *Aster alpigenus, Erigeron peregrinus,* and *Potentilla flabellifolia* are all sensitive to trampling disturbance in the generally sensitive *Valeriana* vegetation type. In the more resistant *Phyllodoce* and *Carex* types, however, they are all resistant. Apparently resistant associates protect these species to some extent, so that higher levels of trampling are required to eliminate them. All species found in more than one vegetation types were more resistant in the type that was generally more resistant, although only these three were classified differently.

Factors That Influence Resistance and Resilience

A number of factors may influence the durability of vegetation types. High-elevation ecosystems, particularly those above tree line, are often characterized as being highly fragile (e.g., Leonard *et al.* 1981). It is interesting to note that these data do not support that conclusion. The most resistant vegetation types were the ones at the highest and lowest elevations—*Carex* and *Pachistima.* As has been reported elsewhere (Cole 1985), the resistance of vegetation types to damage is generally unrelated to elevation.

It has also been suggested, however, that higher elevation ecosystems are likely to have little resilience because their growing seasons are so short (Cole 1987). Again, the data do not support this conclusion. The least resilient vegetation type was the lowest elevation type (*Pachistima*) and intermixed vegetation types, *Phyllodoce* and *Valeriana,* varied greatly in their resilience. Perhaps if the intensity of damage had been more severe, the higher elevation types would have required more lengthy recovery periods. For example, we suspect that if *Carex nigricans* was trampled enough to eliminate all cover and kill all roots that recovery would have occurred only very slowly.

The factors that appear to best explain durability are morphological characteristics of constituent species. The primary strategies for resisting trampling damage are to avoid being stepped on, to be cushioned against impact, or to have tough or flexible aerial parts. Therefore, characteristics that promote resistance include short stature, large size (too large to be stepped on), tufted or bunched habits of growth, stems that are woody or wiry and flexible, and leaves that are tough and/or growing in basal rosettes. Moreover, the resistance of any species will be increased by growing (1) in proximity to other plants that are taller and more resistant (e.g., *Potentilla flabellifolia* in the *Phyllodoce* type) or (2) on a substrate that cushions the impact of trampling (e.g., *Veronica cusickii* growing in a *Carex* turf). Resistant vegetation types tend to be dominated by either tall, tough, woody shrubs (e.g., *Pachistima myrsinites*) or graminoids that grow in bunches or as a turf (e.g., *Carex nigricans*). Low, woody species with brittle stems (e.g., *Phyllodoce empetriforms*) resist low levels of trampling but are sensitive to high levels. Sensitive vegetation types tend to be dominated by broad-leaved herbaceous species with erect, caulescent stems (e.g., *Valeriana sitchensis*).

The primary strategy of resilient species is the ability for rapid regrowth from perennating tissues that can survive trampling. The characteristics that promote resilience are perennating tissues at or below the ground surface that are tough enough to survive trampling or are hidden or cushioned from trampling impact. Resilient vegetation types tend to be dominated by fast-growing broad-leaved herbaceous species (e.g., *Valeriana sitchensis*) or by tufted or turf-producing graminoid species (e.g., *Carex nigricans*).

Trampling by recreationists can be a significant disturbance agent, particularly in parks and wilderness areas where nature preservation is a primary objective. Vegetation types vary greatly both in the ease with which they are damaged and in their ability to recover from damage. Generally the most durable types are dominated by graminoids. Shrubby understories are often resistant to damage, but once damaged, recovery can occur slowly. Broad-leaved herbaceous understories are readily damaged, but capable of rapid recovery. Individual species within the same vegetation type may vary greatly in durability. Land managers need to keep these various capabilities in mind when trying to plan for visitor use.

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Variations in Recharge at the Hanford Site

Abstract

Recharge from meteoric sources (rain and snowmelt) is an important hydrologic variable. A knowledge of recharge rates is needed in the assessment of potential groundwater contamination problems at the U.S. Department of Energy's Hanford Site, near Richland, Washington. Lysimeter data, collected at a number of locations at Hanford over a period of 20 yrs, indicate that recharge rates vary widely, ranging from more than 100 mm/yr to rates near zero (i.e., no measurable drainage). This wide range in recharge is attributed to variations in precipitation, vegetative cover, and surface soil-type. Coarse-textured soils without plants yield the most recharge, fine-textured soils with or without plants yield the least. Deep-rooted plants, such as sagebrush, are generally successful in limiting recharge on all soils at Hanford to near-zero amounts, but shallow-rooted plants such as cheatgrass appear unable to prevent recharge. Drainage (i.e., recharge) from a cheatgrass-covered lysimeter, backfilled with sandy soil, averaged 62 mm/yr (35% of the annual precipitation) during a 3-yr test (1984 to 1986).

The time required for contaminants to travel through the thick unsaturated zone at Hanford is estimated to range from thousands of years, for recharge rates below 1 mm/yr, to tens of years, for recharge rates above 50 mm/yr. The implications of these findings to environmental cleanup and management at Hanford are significant. Present practices that replace surface soils with coarse sands and gravels and prevent or limit vegetative growth are inducing significant recharge that may contribute to contaminant migration. Remediation, such as covering waste sites with a silt-loam soil layer, may be required to limit recharge to negligible amounts, thus ensuring long-term protection of groundwater.

Introduction

Isolation of radioactive wastes in dry sediments high above the water table (i.e., in the vadose zone), has been considered a viable disposal option for Hanford's defense wastes (USDOE 1987). Public acceptance of an in-place disposal option depends, in part, on clearly demonstrating that the wastes will remain hydrologically isolated for thousands of years because some waste components (e.g., technetium, iodine) have very long half-lives. To be hydrologically isolated, the waste zone must be located where meteoric water does not penetrate below the plant root zone and travel to the water table. Such water is termed recharge and serves as a mechanism for transporting soluble contaminants to the groundwater.

Just how much water from meteoric sources penetrates below the plant root zone? This question has been asked repeatedly over the past 47 years. A committee of the National Research Council (National Academy of Sciences) was formed in 1955 to address issues related to disposing of radioactive wastes in the ground. The committee reviewed the scientific basis for waste disposal activities at Hanford and other arid sites and expressed concerns about the assumption that all precipitation was returned to the atmosphere (via evaporation) and none percolated downward to the water table at such sites. In 1966, this committee reiterated its earlier concerns by stating, "the Council is dubious about the concept that in arid and semiarid lands meteoric water does not percolate downward as far as the water table but instead is lost entirely by evaporation and plant transpiration" (NAS 1966). The committee recommended that vadose zone water movement should be thoroughly studied, particularly with reference to questions about percolation of rain and snowmelt to the water table.

In 1985, a panel of university and government experts on hydrology reviewed the recharge question at Hanford (Gee 1987). They shared the concerns expressed previously by the National Academy of Sciences and stated further: "Not withstanding the general aridity of the climate at the Hanford Site and the absence of deep percolation in 'normal years', it is entirely possible that some recharge of groundwater may indeed occur following episodes of high precipitation. Such occurrences are particularly likely under topographic depressions where surface water might accumulate, in places underlain by very coarse and highly permeable deposits, and when the land is denuded of vegetation (as by fire, by overgrazing, or by mechanical clearing)."

In a recent paper, Routson and Johnson (1990) concluded that recharge on the Hanford Site 200 Areas Plateau (where most of the nuclear wastes are stored) is negligibly small (0 ± 2 mm/yr). The basis for this conclusion rests mainly on water stsorage data obtained from one location. At other

locations on the 200 Areas Plateau and elsewhere on the Hanford Site there is mounting evidence that recharge can be large (exceeding 100 mm/yr) under certain circumstances (Gee 1987, Gee *et al.* 1989a, Rockhold *et al.* 1990, Waugh *et al.* 1991).

In this paper, we address the reasons why recharge is so highly variable at Hanford, review the recharge studies published to date, then use recharge estimates to predict the time expected for mobile contaminants to travel through the vadose zone to the underlying water table. We conclude by discussing the implications of recharge variation on waste management practices.

General Considerations

Recharge is controlled by three major factors: climate, soil and vegetation. The assessment of recharge at waste sites at Hanford requires an understanding of the interaction of the three major factors, both under natural site conditions and under conditions that have been disturbed or modified by site operations. Topographical relief can also affect recharge, but most waste processing sites at Hanford are located on nearly flat terrain, and runoff (or runon) is infrequent, thus topography is considered of secondary importance.

Climate

At the Hanford Site the 79-yr-average precipitation is 162 mm/yr. Winters are cool and wet with summers hot and dry (Stone *et al.* 1983). Changes in total precipitation as well as seasonal distribution significantly affect recharge. Since 1970, annual precipitation has varied widely, ranging from 76 mm in 1976 to 281 mm in 1983. In spite of these variations, the 20-yr average of 168 mm is just slightly more than the 79-yr average. Periods exceeding 65 days without rain have been recorded twice in the last 4 yrs (1988 and 1991), while storm events such as thundershowers (with intensities greater than 11 mm in 10 min) have also been recorded in the recent past (1991).

Under Hanford climate, most of the water available for recharge comes in the winter months, during periods of low evaporation. In addition to winter rains, snowmelt can be an important contributor to recharge at Hanford. Rapid snowmelt has been observed to cause high rates of water infiltration into soils resulting in significant drainage (recharge). For example, in February 1985, a warm "chinook" wind, gusting to 72 km/hr, melted most of a 200 mm (approx. 8 in.) snow pack in less than one day, causing significant runoff in some locations and infiltration in others (Gee and Hillel 1988).

Soils

Surface soils on the 200 Areas Plateau at Hanford are predominantly coarse-textured alluvial sands, covered by a variably thick mantle of wind-deposited fine sands (Hajek 1966), and are associated with the Quincy soil series (mixed, mesic Xeric Torripsamments). These surface soils have high infiltration capacities, thus rains infiltrate readily with little or no surface runoff. Subsurface sediments are well-drained coarse sands and gravels of glacial-fluvial (flood) origin (classed informally as the Hanford formation). These sediments overlay compacted silts and clays of the Ringold Formation (Tallman *et al.* 1979). On the 200 Areas Plateau (Figure 1) the water table (located near the top of the Ringold Formation) is as much as 100 m below the land surface (USDOE 1987).

Vegetation

Vegetation consists of shrub-steppe plant communities composed of winter and summer annual grasses and perennial grasses and shrubs (Rickard and Vaughan 1988). This desert vegetation, because of its mixture of shallow and deep-rooted plants, is generally very efficient in utilizing soil water. Winter annuals such as poa (*Poa sandbergii* Vasey) or cheatgrass (*Bromus tectorum* L.) have roots that extend only a fraction of a meter into the soil (Link *et al.* 1990). While winter annuals are efficient in competing for water stored near the soil surface, they cannot access water below their shallow roots. Lack of water coupled with increased temperature cause these grasses to produce seed and die in late spring. A mantle of dead biomass (leaves, stems, etc.) from these grasses persists as ground cover during summer and fall and contributes to frequent and extensive wildfires at Hanford (Rickard and Vaughan 1988).

Perennial shrubs, including sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush (*Chrysothamnus nauseosus* Pallus), and bitterbrush (*Purshia tridentata* Pursh), as well as summer annuals, such as russian thistle or tumbleweed (*Salsola kali* L. var. *tenuifolia* Tausch) and bursage (*Ambrosia acanthicarpa* L.) are common to the site and have extensive root systems (Klepper *et al.* 1985). The perennial shrubs and summer annuals suffer summer water stress but generally survive during the summer months, utilizing both summer rains and water stored at depth in the soil profile from winter precipitation.

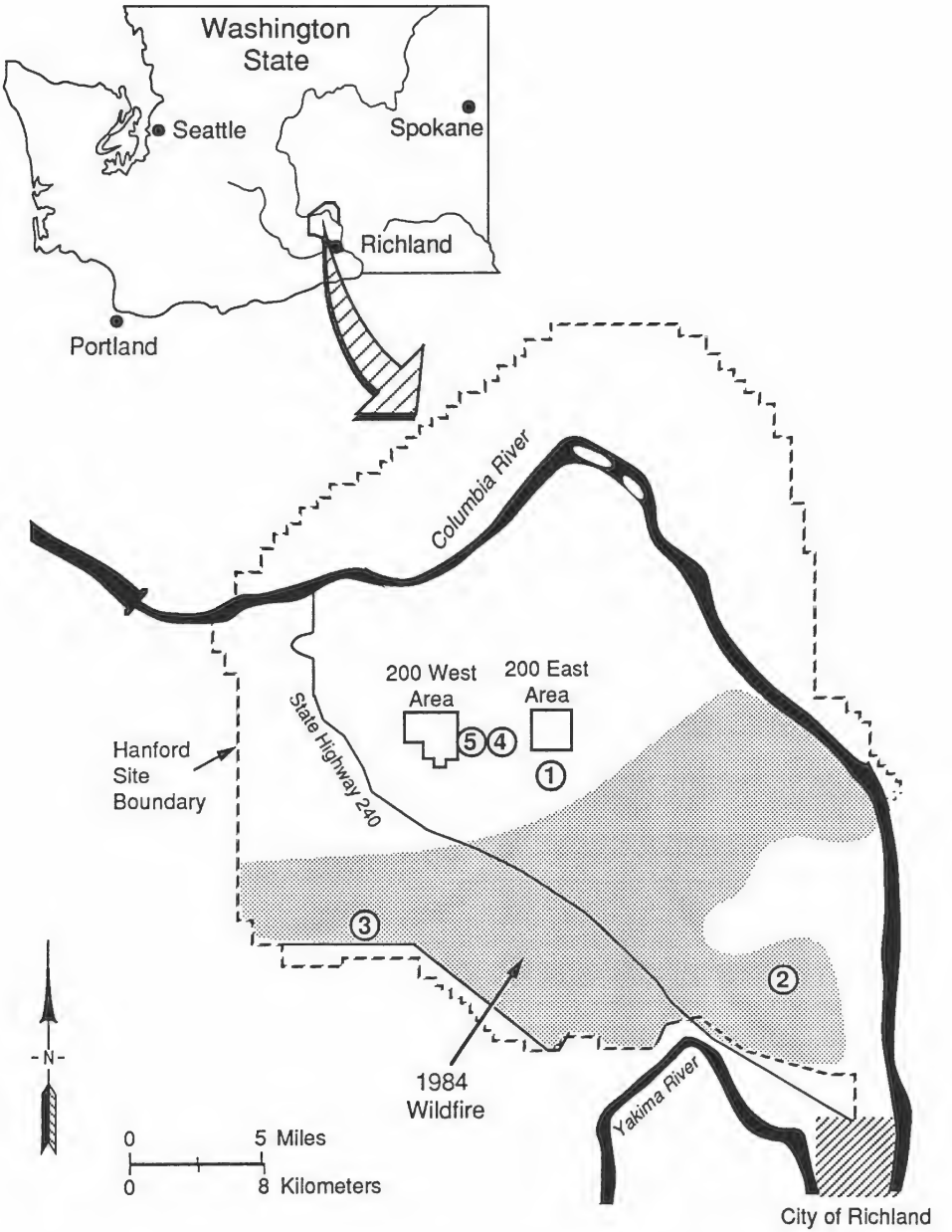

Figure 1. Hanford Site map. Numbered circles represent lysimeter locations. Shaded area represents extent of August 1984 wildfire.

Climate/Vegetation Interactions

Vegetation changes in response to climate at Hanford are relatively common. Over the years there have been periods of drought and periods of excess winter precipitation which have affected species composition. In addition, there have been numerous wildfires which have dramatically altered plant communities at Hanford (Rickard and Vaughan 1988). For example, as shown in Figure 1, a wildfire in 1984 swept over Rattlesnake Mountain and eastward to the Columbia River, burning more than 518 km^2 (over one-third of the entire Hanford Site) (Price *et al.* 1986). Sagebrush does not resprout after fires, so for the past 8 yrs a significant part of the burned area has remained shrubless, covered primarily with cheatgrass. In the burned area it is expected that recharge potential has increased, since water stored at depth from winter rains has likely drained below the root zone of the shallow-rooted grasses.

Surface Disturbances

Site operations have had a significant impact on recharge through changing the surface soil and vegetative conditions at specific waste sites. As an example, since 1947, many large storage tanks (ranging in size from 55 thousand- to 1 million-gallon capacity) have been buried in the 200 Areas at locations called "tank farms" (USGAO 1989). During excavation of the tank farms, both vegetation and surface soil were removed. Backfill, which now covers the tanks to a depth of about 2.5 m, consists of very coarse sands and gravels (Smoot *et al.* 1990). The coarse-textured surface combined with an absence of vegetation (via herbicide application) optimizes conditions for recharge.

At other locations in the 200 Areas, where liquid and solid wastes have been buried, the surfaces often have been covered with soil and revegetated, primarily with a variety of grasses (Fuchs and Cox 1983). There are no detailed studies of soil type or plant rooting depth at these waste sites, so it is difficult to estimate recharge conditions at these sites. However, the transplanted grasses at these sites have, in general, shallower roots than the original cover (shrubs, etc.), thus we would expect the recharge potential to have increased.

Recharge Methodology

The wide range of changing surface conditions has given rise to a wide range of recharge that is only now being documented. Quantification of recharge can only be indirect since the deep water table and lack of surface water (streams, etc.) preclude direct measurements. Tracer techniques and lysimeters are two approaches that have been used to estimate recharge conditions on the 200 Areas Plateau and elsewhere at the Hanford Site.

Initial Studies

There were several research studies initiated at the Hanford Site in the late 1960s and early 1970s designed to address the question of natural (meteoric) recharge in the 200 Areas. One of the studies measured bomb-pulse tritium distributions in the soil. Another study focused on water balance measurements in lysimeters.

Tritium Profiles

From 1953 to 1969, significant quantities of tritium were released to the environment during atmospheric testing of thermonuclear weapons (i.e., hydrogen bombs). Tritium removed from the atmosphere during precipitation events was deposited on the land surface in pulses in the 1950s and 1960s. The downward migration of these tritium pulses should indicate the depth of penetration of recent recharge. Based on consistently elevated levels of tritium found in near-surface sediments (Brownell 1971), there is an indication that meteoric water moved to depths of about 5 m during a 16-year period. However, the tritium fallout study was marred by non-replicated sampling, possible cross-contamination, and poor vertical resolution.

Lysimeter Studies

Lysimeters are simply soil-filled containers of various sizes and configurations which can be used to measure water (and solute) flow through soil. Lysimeters, as used under field conditions, are generally set vertically in the ground with the top open and flush with the surrounding soil surface. The lysimeter soil responds to the precipitation incident on it and the water balance (i.e., precipitation balanced against evapotranspiration, water storage, and drainage) reflects the surface conditions of the lysimeter. Under appropriate circumstances lysimeter data can be useful in estimating recharge (Gee and Jones 1985). Generally, the larger (and deeper) the lysimeter, and the more similar the lysimeter surface soil and vegetation are to the surroundings, the better the estimate of recharge.

The first study of recharge using lysimeters was conducted at the Hanford Site in 1971 (Hsieh *et al.* 1973). Two 18-m-deep lysimeters, one closed at the bottom, the other open, were installed on the 200 Areas Plateau in a location that is about 2 km directly south of the 200-East Area (Figures 1 and 2). To our knowledge these are the deepest lysimeters in the world. As indicated by Brownell *et al.* (1975), "the general plan of the lysimeter experiment was to use the closed-bottom lysimeter as a container to collect water, if it does indeed tend to percolate to the water table on the 200 Areas Plateau of the Hanford site." Measurements of water content in the closed-bottom lysimeter could then be interpreted as an indication of the presence or absence of recharge. Increased water content in the bottom of the lysimeter would result only if water had percolated to the bottom over the period of the study. Stable or decreasing water contents would indicate lack of recharge.

The lysimeters were filled with sediment which had been excavated from the site and thoroughly mixed using a road construction batch-plant located nearby (Hsieh *et al.* 1973). Gee (1987) reported that the sediment in the closed-bottom lysimeter had a sand texture (87% sand, 10% silt and 3% clay). This is very similar to the texture of core sediments taken from four wells adjacent to the lysimeters (Routson and Johnson 1990). Downwell access tubing was installed for monitoring water content profiles using fast-neutron-moderation techniques. Monitoring of the lysimeters was initiated in early 1972 and continued on a routine basis for a period of about 7 yrs (Brownell *et al.* 1975, Last *et al.* 1976, Jones 1978).

Detailed records of vegetation were not kept for these lysimeters. Routson and Johnson (1990) suggest that the lysimeter surfaces were relatively free of vegetation from 1972 through 1980. However, Gee and Heller (1985) show photographs of the lysimeters taken in 1974 and 1978 with vegetation (presumably tumbleweed) growing on the lysimeter surfaces. We assume from photographic records and periodic visits that some vegetation was present on the lysimeters during much of their history.

Interpretation of the neutron logs by several researchers (Brownell *et al.* 1975, Last *et al.* 1976 and Jones 1978) suggested that if meteoric water was moving deep into the closed-bottom lysimeter, it was doing so very slowly. Below the 5-m depth the water content stayed relatively constant at about 0.06 cm^3/cm^3. Jones (1978) suggested that the constant water content implied a unit hydraulic gradient (i.e., gravity drainage) condition. Jones used the data of Hsieh *et al.* (1973) and calculated the unsaturated hydraulic conductivity at a water content of 0.06 cm^3/cm^3, which he used to estimate a steady-state recharge rate of approximately 5 mm/yr.

Subsequent Studies

Since the 1970s, studies of recharge have continued. Model development and use of additional lysimeter facilities have increased our understanding of recharge processes at Hanford. Figure 1 shows the location of the additional lysimeter studies. Both modeling and lysimeter studies have been used to document recharge under a range of soil and vegetative conditions, including the conditions at the 200-East Lysimeter site.

Modeling of the Closed-Bottom 200-East Lysimeter

To determine the role of vegetation in controlling water balance, Fayer *et al.* (1986) used the UNSAT-H computer code to model the 200-East closed-bottom lysimeter. The UNSAT-H code embodies a finite-difference model that solves transient, unsaturated water flow problems. With the UNSAT-H code, they simulated the daily water balance of the closed-bottom lysimeter, with and without vegetation, for the 14-yr period from January 1972 to December 1985. Inputs to the model were daily historical weather variables (precipitation, solar radiation, maximum and minimum air temperature, relative humidity, wind speed), soil hydraulic properties, and a plant algorithm that accounted for uptake of water by vegetation. Plant-cover estimates ranged from 0% in 1972 and 1973 to a maximum of 30% in 1978 (based on photographic evidence). Seasonal growth was simulated by initiating water uptake in late spring and summer, and allowing the plant to extend roots to a depth of 3 m over the course of each summer.

Figure 3 shows the simulation results reported by Fayer *et al.* (1986). Simulated water storage increased 175 mm when no plants were present and decreased 28 mm when plants were present. The simulated water storage with plants is in reasonable agreement with the value calculated from the core data obtained in October 1985 and reported by Routson *et al.* (1988).

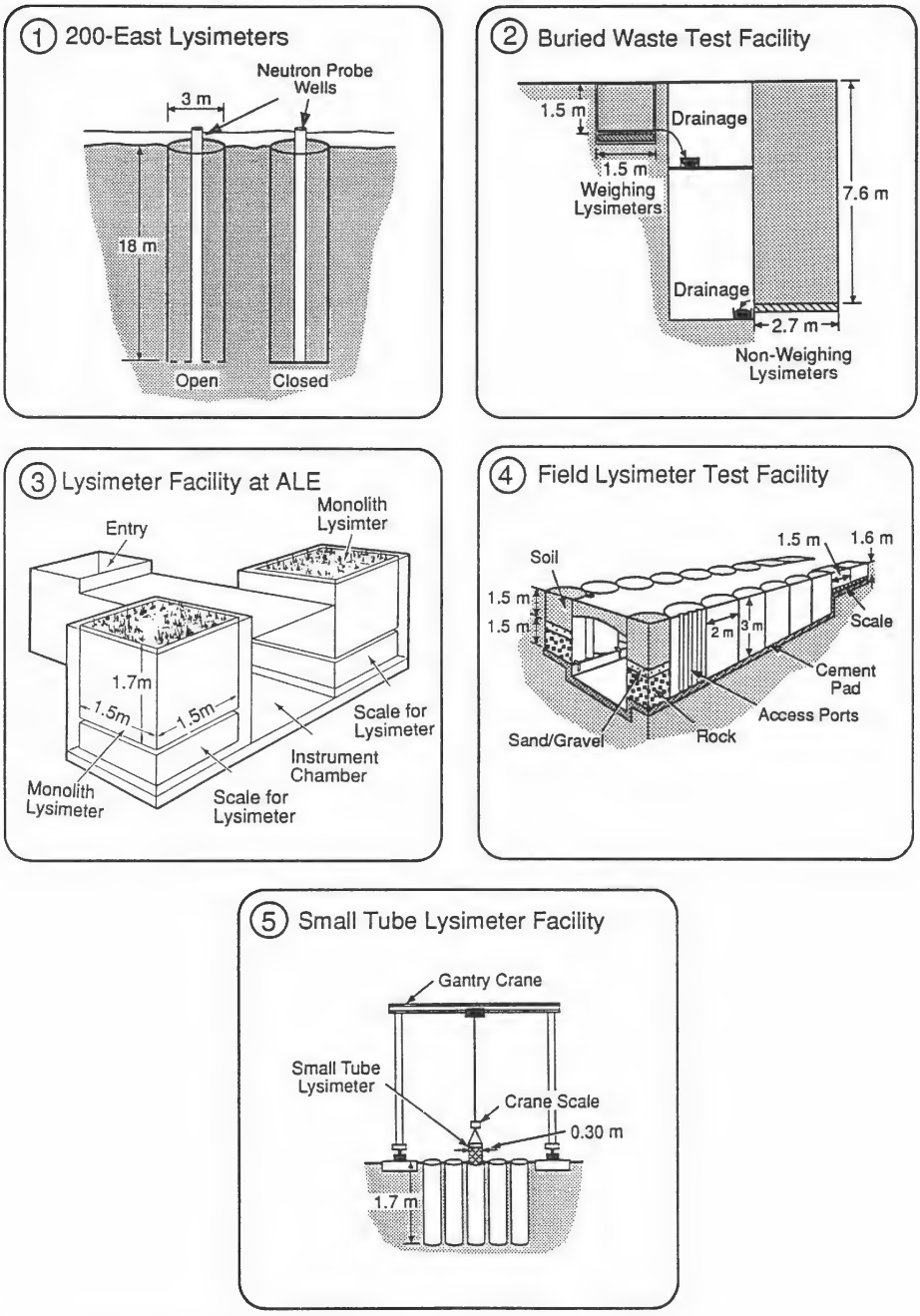

Figure 2. Schematics of lysimeter facilities. Numbered circles are locations shown on Figure 1.

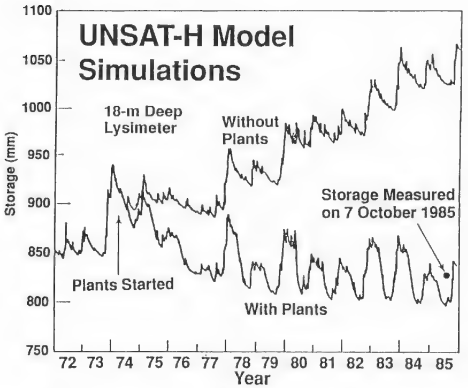

Figure 3. Predicted and observed water storage at the 200-East closed-bottom lysimeter.

Additional 200-East Lysimeter Measurements

Routson *et al.* (1988) collected samples for water content analysis by coring the closed-bottom lysimeter in October 1985. They found low water contents that compared favorably with water contents measured during filling operations in 1971. They also observed no increase in water content at the bottom of the lysimeter and only slight changes in water content below the 3-m depth. From the measured differences in water contents between 1971 and 1985, Routson *et al.* (1988) concluded that the drainage (recharge) at this location was negligibly small (0 ± 2 mm/yr).

In Janary 1988 a visit was made to the 200-East lysimeters. The open-bottom lysimeter had been partially excavated and could not be monitored. We found the rim of the closed-bottom lysimeter buried beneath about 20 cm of soil and the surface vegetated with mostly annual grasses and weeds. While removing the soil down to the lysimeter rim we discovered that the roots of scurf pea (*Psoralea lanceolata* Pursh), a desert lentil with a prolific root system, were abundant in the soil above the lysimeter as well as outside the lysimeter (Gee *et al.* 1989a). Brownell *et al.* (1975) indicated that the rim was buried more than 15 cm beneath the soil surface at least as far back as 1975. Thus, even if plants were specifically removed from the surface directly above the lysimeter, roots from plants outside the lysimeter could have accessed the water within the lysimeter.

Figure 4 shows the observed changes in water storage compared to changes in surrounding

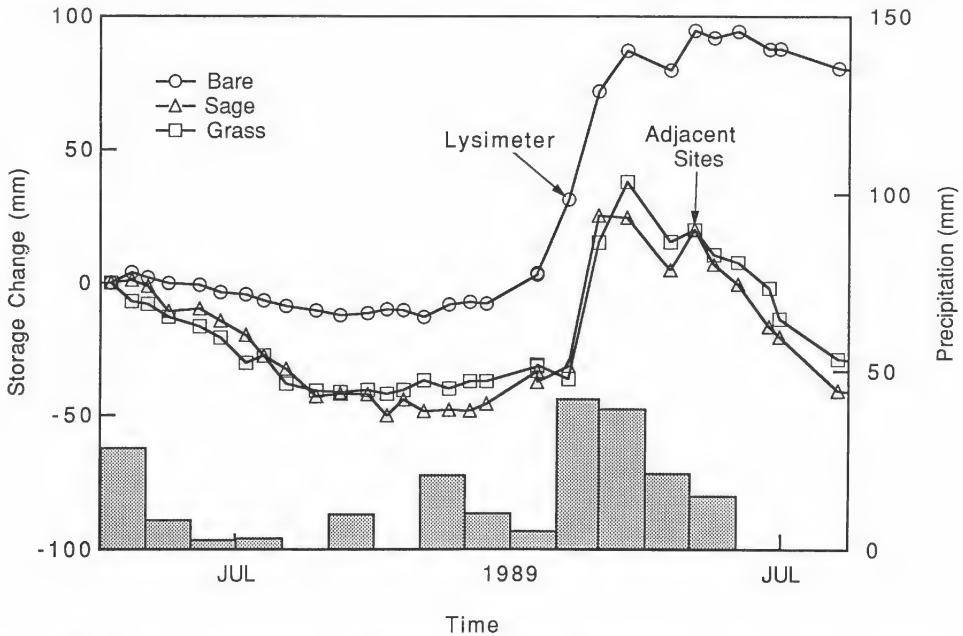

Figure 4. Measured water storage changes at the 200-East closed-bottom lysimeter and adjacent sites. Bar graphs represent monthly precipitation.

vegetated sites (Rockhold *et al.* 1990). The data clearly show differences in water removal by bare and vegetated surfaces. The data also show the effects of winter rain on water accumulation in the soil. In the bare surface lysimeter the water stored from winter rains in late 1988 and early 1989 are not removed from the profile. At adjacent locations where plants (grass and shrubs) were growing on the soil surface, the winter rains were entirely removed by late spring. The data are in qualitative agreement with the model predictions by Fayer *et al.* (1986). The lack of recharge suggested by the 1985 coring data of Routson *et al.* (1988) does not appear to be due to evaporation alone, but rather to the combination of evaporation and transpiration. If plants are removed from waste sites with soils similar to (or coarser than) the sands found in the 200-East lysimeter, we would expect water storage (and thus recharge) to increase.

Buried Waste Test Facility Lysimeters

Figure 2 shows the configuration of the Buried Waste Test Facility (BWTF) which has been in operation since 1978 (Rockhold *et al.* 1990). A suite of lysimeters at this facility are used to measure the water balance of unvegetated and vegetated sands. Drainage lysimeters (2.7-m dia. by 7.6-m deep) and weighing lysimeters (1.5 m by 1.5 m by 1.5-m deep) have been used to monitor drainage at this site for the past 13 yrs.

Table 1 shows that drainage from the weighing lysimeter with a cheatgrass cover was about 35% of the annual precipitation for a 3-yr period

TABLE 1. Summary of estimated recharge from lysimeter facilities at the Hanford Site.

Facility[a]	Soil/Vegetation	Irrig.	Time	Recharge Estimate (mm/yr)	Recharge Estimate (% of Precip.)	Ref.[b]
200-East	Sand/Tumbleweed	No	1971-1985	<2	<1	1
200-East	Sand/Bare	No	1988-1989	90	43	2
BWTF	Sand/Bare	No	1985-1986	111	48	2
BWTF	Sand/Bare	No	1986-1987	102	55	2
BWTF	Sand/Bare	No	1987-1988	40	29	2
BWTF	Sand/Bare	No	1988-1989	42	24	2
BWTF	Sand/Cheatgrass	No	1984-1986	62	35	3
BWTF	Sand/Tumbleweed	No	1986-1987	1	5	2
BWTF	Sand/Tumbleweed	No	1987-1988	0[c]	0	2
BWTF	Sand/Tumbleweed	No	1988-1989	10	6	2
ALE	Silt Loam/Sagebrush	No	1986-1990	0[c]	0	4
ALE	Silt Loam/Bunchgrass	No	1986-1990	0[c]	0	4
FLTF	Silt Loam/Bare	Yes	1987-1990	0[c]	0	5
FLTF	Silt Loam/Bare	No	1987-1990	0[c]	0	5
FLTF	Silt Loam/Sagebrush	Yes	1987-1990	0[c]	0	5
FLTF	Silt Loam/Sagebrush	No	1987-1990	0[c]	0	5
STLF	Gravel over Silt/Bare	Yes	1988-1989	204	59	6
STLF	Gravel over Silt/Bare	No	1988-1989	74	48	6

[a]200-East = 18-m-deep, Closed-Bottom Lysimeter (Figures 1 and 2)
BWTF = Buried Waste Test Facility-300 Area (Figures 1 and 2)
ALE = Arid Lands Ecology Reserve Lysimeters (Figures 1 and 2)
FLTF = Field Lysimeter Test Facility (Figures 1 and 2)
STLF = Small Tube Lysimeter Facility (Figures 1 and 2)

[b]1—Routson and Johnson (1990)
2—Rockhold *et al.* (1990)
3—Gee (1987)
4—Gee *et al.* (1991)
5—Campbell *et al.* 1991)
6—Waugh *et al.* (1991)

[c]Zero value indicates that no drainage occurred from lysimeter(s).

(1984-1986). Cheatgrass is shallow-rooted (observed rooting depths of less than 1 m under Hanford Site soil conditions) and apparently unable to utilize the winter rains that infiltrated the sandy soil and accumulated below the root zone. The increased storage below the root zone resulted in drainage. In subsequent years, when deeper-rooted plants (e.g., tumbleweed) invaded the lysimeter, water in the lower part of the lysimeter was removed and drainage was reduced significantly. As expected, drainage from lysimeters with no plants was always greater than from the lysimeter with plants. Drainage from bare sand varied with time, ranging from 40 mm/yr to 111 mm/yr, in response to annual fluctuations in precipitation (Table 1).

ALE Lysimeters

Figures 1 and 2 show the location and schematic of four monolith lysimeters that were installed in 1986 at the Arid Lands Ecology (ALE) Site at the north end of Rattlesnake Mountain at an elevation of 300 m above MSL. The monolith lysimeters are boxes approximately 1.5 m on a side, constructed to contain undisturbed, silt loam (mixed, mesic, Xerollic Camborthids) soil (Gee *et al.* 1991). The wildfire of 1984 provided the treatment effect for the lysimeter study of water balance of differing plant communities. Roads in the area acted as a fire break and isolated an undisturbed area adjacent to an area consumed in the burn. One pair of lysimeters contained bunchgrass (*Agropyron spicatum* Pursh.) and were located in the burned area while the other pair contained bunchgrass and sagebrush and were located in the unburned area. Since installation, the lysimeters have been exposed to ambient precipitation which, because of location near Rattlesnake Mountain, is about 230 mm (42% higher than on the 200 Areas Plateau). In spite of plant cover difference and elevated precipitation, none of the lysimeters at the ALE site have drained (Table 1).

Field Lysimeter Test Facility

Figures 1 and 2 show the location and schematic of the Field Lysimeter Test Facility (FLTF), which was constructed near the Hanford Meteorological Station in 1987 to evaluate the use of engineered soil covers (barriers) to limit recharge at waste sites (Gee *et al.* 1989b, Campbell *et al.* 1990). Fourteen of the FLTF lysimeters are 2 m in diameter and 3 m deep. These lysimeters are filled with sediment layers in the following sequence from bottom to top: rock, gravel, sand, and a 1.5-m-thick layer of silt loam soil. The remaining four lysimeters are square boxes (1.5 m x 1.5 m x 1.6 m) filled with 1.5 m of silt loam soil overlying a layer of sand. The boxes rest on large (9.6-Mg-capacity) electronic scales. The soil in the top of all the FLTF lysimeters was excavated from an area about 10 km west of the FLTF, where the soil is classified as Warden silt loam (mixed, mesic Xerollic Camborthids). A typical particle-size distribution for this silt loam is 19 percent sand, 69 percent silt and 12 percent clay.

A series of water balance experiments have been conducted to test various surface conditions, including changes in vegetation (bare soil vs. transplanted shrubs and grasses) and changes in precipitation. The precipitation treatments exposed lysimeters to ambient and enhanced precipitation conditions. The enhanced (320 mm/yr) treatment is twice the annual average precipitation and is higher than any annual amount ever recorded at the Hanford Site. There has been no drainage from treatments with or without plants under ambient or enhanced precipitation (Table 1).

Small Tube Lysimeter Facility

Adjacent to the FLTF there are 105 smaller (0.3-m-diameter by 1.6-m-deep) lysimeters currently in use for water balance studies (Figure 2). These lysimeters, part of the Small Tube Lysimeter Facility (STLF), have been constructed to provide replication of the FLTF treatments and to add additional treatments, including unvegetated, gravel cover to simulate conditions that currently exist at some of the waste sites in the 200 Areas (Waugh *et al.* 1991). The STLF lysimeters, with silt loam soil surfaces, have performed similarly to the larger lysimeters at FLTF; no drainage has occurred from them. The gravel-covered lysimeters have had as much as 50% of the applied water drain through them (Table 1). These data confirm that fine-soil surfaces are effective barriers in preventing drainage under Hanford climate conditions, while coarse soil surfaces are not. Quantification of the rates of drainage continue to be made with these lysimeter facilities. Studies of the effect of significantly increased precipitation (up to three times the annual average) have been initiated and will continue over the next several years to document recharge under conditions of elevated precipitation.

Travel-Time Calculations

Knowledge of recharge rates at the Hanford Site is necessary for calculating contaminant travel times through the vadose zone. Using a simple one-dimensional model, the steady-state water velocity in the vadose zone can be related to the recharge rate as follows:

$$v = r/\Theta \quad (1)$$

Where v = water velocity (mm/yr)
r = recharge rate (mm/yr)
Θ = water content (cm^3/cm^3)

The velocity can also be expressed as

$$v = L/T \quad (2)$$

where L is the travel distance (mm) and T is the travel time (yr). Combining Eqs. (1) and (2) yields the expression for travel time

$$T = L\,\Theta/r \quad (3)$$

For the tritium study of Brownell (1971) we can estimate recharge knowing the timing of the initial tritium pulse (1953), the maximum depth of tritium penetration and the water content of the sediments in which the tritium pulse was measured. Based on the reported gravimetric water contents and assuming a typical bulk density of 1.7 g/cm^3 we estimate an average water content for the sediments was 0.047 cm^3/cm^3. Then using Eq. (1) and the estimated depth of tritium penetration of 5 m in 16 yrs (1954 to 1970), we calculate a recharge rate of 14.7 mm/yr. Given that the tritium can also move as a vapor, the calculated recharge rate represents a conservative estimate (i.e., the actual value for liquid flow may be lower).

Assuming a 60-m-thick vadose zone above a water table, Eq. (1) can be used to calculate that, under the above conditions, with recharge, r, = 14.7 mm/yr and water content, Θ, = 0.047 cm^3/cm^3, a non-sorbing contaminant would reach the water table in 192 yrs. Now suppose that below the 5-m depth to which the tritium penetrated, the sediments were coarser, as is often the case at Hanford (Tallman *et al.* 1979). In coarser sediments the water content would be lower; for example, 0.025 cm^3/cm^3. Water contents this low have been found in coarse, well drained sediments at Hanford (Brownell 1971). Heller *et al.* (1985) indicate that for layered sediments, the overall travel time can be computed as a summation of travel times through the various layers of differing water contents. Thus, while the recharge rate is constant throughout the soil profile, the water velocity through various layers will vary according to their volumetric water content. Summing the travel times through the two layers, the total travel time is 110 years. This is 82 years less than (about one-half) the travel time through a profile with no coarse sublayer.

Our simplified (1-dimensional) analysis does not account for lateral spreading in layered sediments, as might occur following a localized injection of water (e.g., flow from a leaking tank and subsequent spreading of the contaminant plume above a caliche layer).

The travel time analysis suggests that a long-lived, mobile contaminant would reach the water table faster in coarser than in finer sediments. In general, the coarser the soil, the shorter the travel time through the vadose zone for the same recharge rate. In addition, there is mounting evidence that unsaturated flow in coarse sediments can be unstable, such that pulses of water might move in preferred channels or paths at rates far in excess of the average water velocity that would occur in uniformly wetted soils (Hillel 1987, Gee and Hillel 1988). The one-dimensional analysis used here does not take preferential flow into account, so it would not predict potential early arrival (faster flow) that could occur if preferential flow occurs in Hanford sediments.

Travel times through a 60-m-deep sediment profile were computed as a function of recharge rate for three Hanford Site sediments (two sands and a silt loam) following procedures described by Heller *et al.* (1985). Hydraulic properties were determined in the laboratory for the three sediments and were used to determine water contents for a given recharge flux. Then Eq. (3) was used to calculate the corresponding travel times (Figure 5).

The computed travel times provide guidance on recharge control. For example, to exceed a 10,000 yr limit in travel time, the recharge rate in the sands must be below 0.5 mm/yr. For the same travel time in silt loam, the recharge rate must be less than 1 mm/yr. This analysis holds for uniform soils that are subjected to areally uniform recharge rates under steady state conditions. A similar analysis has been reported for layered sediments by USDOE (Appendix Q of the Final Environmental Impact Statement-Disposal of Hanford Defense High-Level, Transuranic and Tank Wastes, Hanford Site Richland Washington; USDOE 1987).

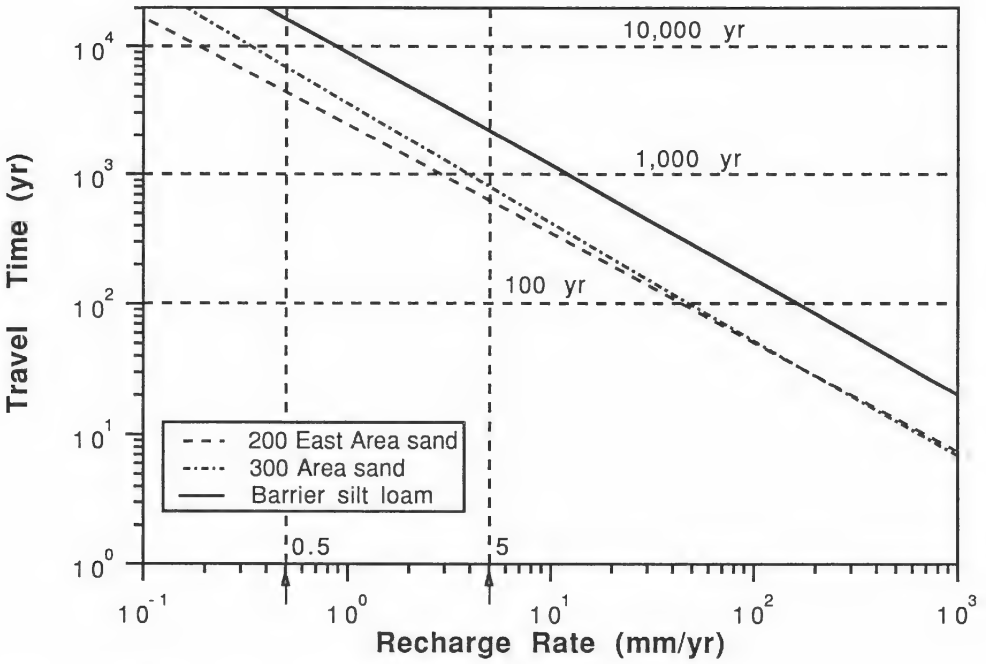

Figure 5. Travel time as a function of recharge in a 60-m-deep vadose zone.

Discussion

The lysimeter drainage data indicate that, regardless of location, drainage (recharge) occurred in both sandy and gravel-covered soils (Table 1). The data indicate that recharge values ranged from more than 100 mm/yr to less than 2 mm/yr in sandy soils (or those covered with gravel) and was estimated to be zero (no measurable drainage) in silt loam soils.

Coarse-Textured Soil

All lysimeter data collected to date suggest that recharge is significant when coarse-textured soils (typical of most of the Hanford Site) are kept free of vegetation. Recent modeling of water flow and contaminant migration at a tank farm, where buried single-shell tanks are located, has shown that annual recharge could be more than 110 mm/yr (70% of the long-term annual precipitation) because the surfaces of coarse sands and gravels are kept free of vegetation (Smoot *et al.* 1990). These modeling results are consistent with lysimeter results presented here. Under such high recharge rates, flow around tanks is accelerated, causing mobile contaminants leaking from the tanks to be moved to the water table at accelerated rates. Model simulations (Smoot *et al.* 1990) show that flow to the water table can occur in tens of years at tank farms or other similar sites where surfaces are bare and gravel covered.

The recharge rate in any one year in bare soils depends on the seasonal distribution of precipitation, with maximum recharge events occurring after the wettest winter periods (Figure 4). Data in Table 1 show a variable amount of drainage occurred in bare sand at the Buried Waste Test Facility (BWTF) over a period of 4 yrs (1985 through 1989). Although there is some lag between precipitation and drainage in the 7.6-m-deep lysimeters at the BWTF, the highest drainage rate (111 mm) is associated with the most annual precipitation (231 mm) and the lowest drainage rate (40 mm) with the least precipitation (134 mm). In soils with a deep (i.e., >90 m) water table, as exists in the 200 Areas Plateau at Hanford, such drainage fluctuations would likely be damped considerably. The recharge in deep sediments then would be an average of multiple years of fluctuating drainage. This suggests that lysimeter data should be taken over

a number of years to produce reliable estimates of recharge.

Vegetation

Vegetation produces a dramatic effect on recharge in coarse-textured soils. At the BWTF site, a sand-filled lysimeter, revegetated with cheatgrass, produced significant drainage (62 mm/yr) during 1984 through 1986, while precipitation averaged 177 mm/yr (Table 1). Invasion of tumbleweed on this lysimeter in subsequent years reduced the drainage to small amounts, ranging from 0 to 10 mm/yr. The data suggest that shallow-rooted plants do not reduce recharge to negligible amounts on coarse-textured soils at Hanford. The data also suggest that deep-rooted plants, such as tumbleweed, may not be entirely effective in eliminating recharge in sandy soils, since in 2 of 3 yrs there was measurable drainage in the sand-filled lysimeter when tumbleweed was present.

The intrusion into waste sites by plant roots is a major concern for waste management at the Hanford Site. Radioactive tumbleweeds have been found growing on waste burial grounds (Dabrowski 1973, Marshall 1987). For this reason plants have been removed by non-selective herbicides and soil sterilants from some waste sites (Dabrowski 1973) and relatively shallow-rooted grass species have been planted on other waste sites (Fuchs and Cox 1983). While effectively limiting radionuclide uptake, the removal of vegetation or the modification of plant species (i.e., changes to shallow-rooted species) tends to enhance recharge.

No drainage was observed in the sandy soil in the 200-East closed-bottom lysimeter for nearly 14 yrs (Figure 2, Table 1). The lack of drainage is attributed to the type of vegetation (deep-rooted annuals and perennials) growing on the lysimeter (from at least 1978 through 1988). When plants were removed from the 200-East lysimeter in 1988, water storage stayed relatively constant until the winter of 1988-1989. In response to late winter and early spring rain, water storage increased by nearly 100 mm so that by July, water storage was over 85 mm more than in early 1988 (Figure 3). In contrast, measurements taken in adjacent grass- and shrub-covered soils showed large water storage losses in the summer of 1988 and even larger losses in 1989. By July of 1989, all of the incident precipitation had been removed by evapotranspiration from the vegetated soils (Figure 4). We conclude that absence of vegetation on the sand-filled lysimeter caused increased storage. Increased storage below the root zone eventually leads to recharge.

Fine-textured Soil

None of the lysimeters containing silt loam soil produced any drainage (Table 1). The lack of drainage was irrespective of location, water application (precipitation and irrigation), or the presence or absence of vegetation. On bare lysimeters at the FLTF, water application rates were as much as 320 mm/yr (twice the long-term annual average). Even under these elevated precipitation conditions, bare, silt loam soil did not drain. Evaporation was able to remove the entire water application over the three year test. With plants, the lysimeters (at both ALE and FLTF locations) dried even further and there was no drainage. The lack of drainage suggests that a surface containing silt soil is ideal for limiting water infiltration under Hanford Site conditions. The optimum soil depth needed to effectively control water infiltration is presently under study (Campbell *et al.* 1991). To date we have measured no drainage in barrier (FLTF) lysimeters containing either a 1-m-thick layer or a 1.5-m-thick layer of silt loam soil.

Summary

Recharge is variable at the Hanford Site, ranging from over 100 mm/yr in bare sands and gravels to near zero (non-measurable) amounts in silt-loam soils. The implications for waste management at the Hanford Site are relatively straightforward. Present conditions (bare, coarse soil surfaces) found at tank farms and other waste sites are conducive to recharge and accelerated contaminant migration. However, waste sites can be managed to greatly reduce recharge and thus significantly increase the time it takes for contaminants to travel to the water table. Vegetation on coarse soils can reduce recharge. Deep-rooted plants, such as sagebrush or tumbleweed are more efficient in utilizing soil water than shallow-rooted plants, such as cheatgrass. Unfortunately, deep-rooted plants can access buried waste and assimilate radioactive and chemical contaminants. For this reason plants are often removed (via herbicides and soil sterilants) from waste site surfaces.

The best cover material for limiting recharge at waste sites appears to be a fine-textured soil, such as the silt loam soil found near the 200 Areas Plateau. Ongoing research is testing how well silt loam soil can perform in reducing recharge under

a range of vegetative and climatic conditions. Tests conducted over the past several years are encouraging and suggest that both vegetated and bare silt loam soil (at least 1-m thick) can effectively limit recharge to negligible amounts, even when the precipitation is at least twice the annual average.

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The Role of Mycorrhizal Fungi in Competitive Interactions Among Native Bunchgrasses and Alien Weeds: A Review and Synthesis[1]

Abstract

The role of vesicular-arbuscular mycorrhizal (VAM) fungi in competitive interactions among native bunchgrasses and alien weeds is reviewed. Brief reviews of the mycorrhizal symbiosis and rangeland ecology provide a background for discussion of the role of VAM fungi in inter- and intraspecific competition in sagebrush-grass systems.

Plants can be significantly better competitors for soil resources when mycorrhizal than when not mycorrhizal, and VAM fungi can alter the outcome of competitive interactions among plants. Additionally, soil resources can be transferred from one plant to another through a network of hyphae produced by VAM fungi; such transport can improve growth in the receiver plant. The response of a plant to the formation of mycorrhizae depends upon the taxa of the plant and fungal symbionts, their phenologies, and on the severity of environmental stress.

Native bunchgrasses of the Intermountain West are mychorrhizal. Alien weeds introduced to the sagebrush steppe include both mycorrhizal and nonmycorrhizal species. When a rangeland site is colonized by nonmycorrhizal species, VAM fungi populations decline. In the absence of VAM fungi, mycorrhizal bunchgrasses are at a competitive disadvantage compared to nonmycorrhizal species in capturing limited soil resources. However, the opposite is also true: mycorrhizal species out-compete nonmycorrhizal species when VAM fungi are abundant.

One naturalized alien, cheatgrass (*Bromus tectorum*), is a facultative host of mycorrhizal fungi. Cheatgrass is an effective competitor in the rangeland environment, and its relative competitive ability, compared to native bunchgrasses, is unlikely to be altered by VAM fungi. Though mycorrhizal fungi would enhance the competitive ability of native bunchgrasses, cheatgrass would reap comparable or greater benefit since it also hosts VAM fungi and, due to a rapid rate of growth, acts as a strong sink for soil resources. This is probably one of the factors behind continued, long-term occupancy and/or dominance of rangeland sites by cheatgrass.

However, it is not unreasonable to expect greater efficiency among coevolved mutualists compared to a profiteering alien. If assimilates are more efficiently transferred from a native bunchgrass to its progeny, then VAM fungi have an important role to play in the restoration of Intermountain rangelands. Research into the role of mycorrhizal fungi in competitive interspecific interactions, rhizosphere community dynamics, the mycorrhizal dependence of rangeland grasses, and patterns of translocation is needed before definitive answers can be presented.

Introduction

This review examines the role of vesicular-arbuscular mycorrhizal (VAM) fungi in the dynamics of sagebrush-grass communities, with particular attention to the possible role of VAM fungi in mitigating interspecific interference. I begin with a brief review of the mycorrhizal symbiosis and an introduction to rangeland ecology. These sections lay the groundwork for examining the role of VAM fungi in ameliorating the competitive superiority of alien species that have invaded western rangelands. Though much research remains to be conducted in this area of community ecology, evidence compiled over the last 15 years suggests an important, possibly essential, role for VAM fungi in the population dynamics of native bunchgrasses.

The Mycorrhizal Symbiosis

Vesicular-arbuscular mycorrhizal fungi are common in terrestrial ecosystems, forming obligatory symbioses with most higher plants (Read *et al.* 1976, Mosse *et al.* 1981). The correlation between taxa and the symbiotic habit is strong. For example, members of the family Graminae typically host VAM fungi (are mycotrophic), whereas the families Cruciferae and Chenopodiaceae generally do not (are nonmycotrophic) (Trappe 1981, Pendelton and Smith 1983, Newman and Reddell 1987). However, mycorrhizal dependency varies within all plant families. Some chenopod taxa, for example, may be briefly mycorrhizal during their life cycle (Trappe 1978, Allen and Allen 1990). Additionally, pioneer or ruderal species are more frequently nonmycorrhizal than are perennial species (Trappe 1987).

Mycorrhizal fungi often play a vital role in the mineral nutrition of a host plant (Trappe 1981), increasing the amount of both macro- and micronutrients acquired (Read *et al.* 1985, Killham 1985, Smith *et al.* 1986). Commonly, VAM fungi improve the host's phosphorus nutrition, particularly when soil phosphorus is limiting (Smith *et al.* 1986, Schubert and Hayman 1986). Drought

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tolerance in herbaceous species has also been improved with colonization by VAM fungi (Allen and Allen 1984, 1986). The host plant benefits since mycorrhizal fungi function as an extension of the host's root system, increasing the efficiency with which a soil volume is exploited (Koucheki and Read 1976, Schubert and Hayman 1986). In exchange, the fungal symbiont(s) obtains carbon from the host plant (Snellgrove *et al.* 1982, Paul *et al.* 1985).

The outcome of competitive interactions between plants can be markedly influenced by VAM fungi (Allen and Allen 1986, Grime *et al.* 1987). For example, Fitter (1987) found inoculation with mycorrhizal fungi to alter the outcome of competition for soil phosphorus and potassium between velvetgrass (*Holcus lanatus*) and perennial ryegrass (*Lolium perenne*). In the absence of VAM fungi, the two species were roughly equivalent competitors. However, given mycorrhizae, velvetgrass clearly emerged as the more successful contestant, sequestering roughly twice as much of each nutrient as did ryegrass.

In natural communities, hosts are colonized by VAM fungi shortly after germinating, often while still in the cotyledon stage and frequently by more than one species of VAM fungi (Read *et al.* 1976, Chiariello *et al.* 1982, Dodd and Jefferies 1986). Host plants may be colonized by germinating VAM fungal spores or contact with the hyphae of VAM fungi or another colonized root. Extensive networks of hyphae, with distributions similar to that of plant roots, are found in undisturbed soils (Mosse *et al.* 1981, Schwab and Reeves 1981).

Mycorrhizal hyphae have been shown to connect host plants of the same and different species (Heap and Newman 1980a, Chiariello *et al.* 1982), and intra- and interspecific transfer of nutrients, both from host to fungi and between different hosts of a fungal symbiont via mycorrhizal hyphae, has been documented (Ho and Trappe 1973, Heap and Newman 1980b, Francis and Read 1984, Grime *et al.* 1987). Neighboring mature individuals may subsidize the early growth of seedlings, particularly shaded seedlings, through a hyphal network, thereby increasing the probability of successful establishment and survival (Francis *et al.* 1986).

Whittingham and Read (1982) investigated nutrient transfer via mycorrhizal hyphae using sheep fescue (*Festuca ovina* L.). Roots of a source plant were split among two halves of a divided pot, and source plants were either colonized by VAM fungi or lacking mycorrhizae. Sink plants were added to one side of the pots, and either distilled water or a nutrient solution containing ^{32}P was added to the other side. When source plants were mycorrhizal, significantly more phosphorus was transferred to sink plants. The relative growth rates of seedlings (sinks) in the nutrients + mycorrhizae, water + mycorrhizae, and nutrient only treatments were 0.1138, 0.0692, and 0.0319, respectively. At 18 weeks, seedlings from the nutrient + mycorrhizae treatment had dry weights three times that of any other treatment. Similar results were obtained by Grime *et al.* (1987) using labeled carbon. Mycorrhizal plants obtained ^{14}C from source plants, while nonmycorrhizal plants in the same pot did not take up the label. Francis *et al.* (1986) concluded that nutrient transfer to seedling sinks via VAM hyphae was sufficient to "sustain significant enhancement of both growth and nutrient composition."

Recruitment of seedlings and species diversity decline in the absence of VAM fungi, particularly during secondary succession (Grime *et al.* 1987, Gange *et al.* 1990). The early establishment phase may be the period in a host's life cycle when it is most dependent upon the fungal symbiont (Mosse *et al.* 1981).

Benefits to hosts of VAM fungi are potentially great in nutrient poor soils and extreme environments, where the symbiosis acts to ameliorate plant stress (Molina *et al.* 1978, Miller 1979, Bethlenfalvay *et al.* 1984, Allen and Allen 1986) and where plants exhibit a stress-tolerant (*sensu* Grime 1977) strategy. In stressful environments, mycorrhizal species are likely to enjoy a competitive advantage over nonmycorrhizal species (Doerr *et al.* 1984, Fitter 1985).

Rangeland Ecology

The Intermountain West features large expanses of semi-arid rangeland supporting sagebrush-grass plant communities (e.g., Franklin and Dyrness 1973, Daubenmire 1970). These communities often include an overstory of western juniper (*Juniperus occidentalis*) and sagebrush (*Artemisia tridentata*), with numerous grasses and forbs in the understory. Annual alien weeds, such as cheatgrass (*Bromus tectorum*), are also common. Apparently, the native species are mycorrhizal (Williams and Aldon 1976, Molina *et al.* 1978, Trappe 1981,

Pendelton and Smith 1983, Doerr *et al.* 1984, Schwab and Loomis 1987, Benjamin and Allen 1987).

Settlement greatly altered the vegetation of sagebrush-grass systems. Since the native bunchgrasses of western rangelands evolved without selective pressure from large herbivores, the effect of livestock on these bunchgrasses was particularly detrimental (Mack and Thompson 1982) since grazing occurred every year and often year round (Strong 1940, Galbraith and Anderson 1971). Native perennial bunchgrasses generally declined in abundance and cover as grazing by introduced livestock increased (Pechanec *et al.* 1937, Mack and Thompson 1982). Fire suppression also altered vegetation dynamics and nutrient cycling in rangeland communities (Burkhardt and Tisdale 1976, Wright *et al.* 1979).

Subsequent to the introduction of livestock, the introduction of cheatgrass and other competitive aliens resulted in an invasion of western rangelands at a rate and to an extent so great that it has become a classic in the literature of biological invasions (e.g., Mack 1981). Rangeland plant community dynamics were fundamentally altered by these alien introductions (Piemeisel 1951, Harris 1967, Young *et al.* 1972).

Prior to these introductions, sagebrush-grass systems were dominated by competitive, stress-tolerant (sensu Grime 1977) perennial bunchgrasses, such as bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*), and sagebrush (Driscoll 1964, Daubenmire 1970). Following the introductions, rangeland communities have come to be dominated by woody species, such as western juniper, and the understory may be dominated by competitive alien annuals as well (Piemeisel 1951, Young *et al.* 1972, Allen and Knight 1984). Many of the introduced annuals are nonmycorrhizal (Trappe 1981, Allen and Allen 1980, Pendelton and Smith 1983).

Typically, early seral alien annuals, such as Russian thistle (*Salsola kali*), enable the establishment of cheatgrass (Piemeisel 1951), a winter annual which does poorly on bare soil (Evans and Young 1984). Cheatgrass is a facultative host of VAM fungi. When cheatgrass grows in communities of nonmycorrhizal plants, it is nonmycorrhizal; in the presence of mycorrhizal plants, cheatgrass is mycorrhizal (Trappe 1981, Pendelton and Smith 1983). Since the native perennial bunchgrasses are mycorrhizal, and since alien annuals are predominantly nonmycorrhizal, belowground dynamics have changed along with plant community dynamics.

Competition, Succession and Mycorrhizae

Succession in sagebrush-grass communities now includes an early seral stage where community composition is dominated by nonmycorrhizal species, and this stage may last from two to more than six years (Piemeisel 1951, Allen and Knight 1984, Biondini *et al.* 1985). The early seral alien species are displaced by cheatgrass, which may or may not be mycorrhizal, and cheatgrass dominance of the understory can last for 20 or more years. When composition of the plant community is predominantly nonmycorrhizal, VAM fungi decline in abundance (Reeves *et al.* 1979), and VAM fungi populations remain depressed until host plants become re-established (Miller 1987, Biondini *et al.* 1985). Moorman and Reeves (1979) found soil from an alien-dominated community to be 40 times less effective as a mycorrhizal inoculant than soil from a nearby sagebrush-grass community; the soil of the alien-dominated community had been severely disturbed three years earlier.

An example of the decline of mycorrhizal fungi populations with invasion by nonmycorrhizal aliens is provided by Russian thistle. Seedlings of Russian thistle responded to colonization of their roots by VAM fungi by sacrificing the colonized cells (Allen *et al.* 1989a). In some cases, the entire vascular tissue of the affected root segment collapsed; less frequently, entire root systems died. Stomatal resistance increased in colonized seedlings, indicating increased water stress probably due to root mortality. When soils were inoculated with VAM fungi, the abundance of Russian thistle declined; Russian thistle density was reduced by a factor of three and cover by a factor of two given inoculation.

Mature Russian thistle is better able to resist invasion by VAM fungi (Schmidt and Reeves 1984, Allen *et al.* 1989a). Even so, some mycorrhizal fungi are able to survive and sporulate beneath Russian thistle, possibly in a parasitic interaction, though spore densities are extremely low (Schmidt and Reeves 1984, Allen and Allen 1990). Thus, in communities dominated by nonmycorrhizal alien annuals, VAM fungi lack both a host and, during the majority of the year, a source of carbon, and

VAM fungi populations decline as a result. The implications for plants dependent upon mycorrhizal fungi are clear; re-establishment of these plant species may not occur until both plant propagules and the spores of VAM fungi occupy the same site at the same time (Doerr *et al.* 1984, Trappe 1988).

The Importance of Shrubs

In rangeland systems, woody shrubs reduce wind velocity at ground level and trap organic debris, soil and snow, and provide shade. Additionally, the phenomenon of hydraulic lift seen in mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) can improve the water relations of neighboring bunchgrasses during summer (Richards and Caldwell 1987, Caldwell and Richards 1989). The result is the creation of "islands" favorable for plant growth (Doescher *et al.* 1984, Allen and MacMahon 1985). Miller (1987) found the presence of shrubs to greatly aid the re-establishment of native perennial grasses in communities dominated by alien annuals.

The spores of VAM fungi are transported with wind blown soil particles in rangelands (Warner *et al.* 1987, Allen *et al.* 1989b) and are, consequently, trapped by shrubs. Biondini *et al.* (1985) found a strong correlation between the re-establishment of rangeland shrubs and the recovery of VAM fungi populations in disturbed soils. The spores of mycorrhizal fungi are thus placed in an environment where the probability of germination and establishment of a host is relatively high. A grass seed germinating beneath a shrub potentially enjoys a greater availability of water and nutrients, moderated microclimate, and the benefits of mycorrhizal symbiosis. Light attenuation by the shrub canopy could potentially reduce growth of the grass, but light is probably not limiting in rangelands, even beneath shrub canopies (Smith and Nowak 1990; Winward 1991).

VAM Fungi and the Competitiveness of Bunchgrasses

The colonization of plants by VAM fungi may have two effects: greater uptake of nutrients and soil moisture by the host, which translates to better growth (Koucheki and Read 1976, Fitter 1977, Killham 1985, Allen and Allen 1986, Schwab and Loomis 1987), and the re-establishment of networks of mycorrhizal hyphae in the soil (Read *et al.* 1976, Whittingham and Read 1982). Once these have happened, mycorrhizal species enjoy a competitive advantage over nonmycorrhizal species in the rangeland environment (Reeves 1985, Ocampo 1986, Miller 1987).

An example of the influence of VAM fungi on the outcome of competitive interactions is provided by Allen and Allen (1984), who grew western wheatgrass (*Agropyron smithii*) and blue grama (*Bouteloua gracilis*) in both monocultures and mixed cultures with Russian thistle. When competing with the alien, both grasses had greater shoot mass and higher stomatal conductance when mycorrhizal than when nonmycorrhizal. Colonization by VAM fungi increased shoot biomass by roughly 25 percent. Mycorrhizal western wheatgrass attained the same shoot biomass when grown in competition with Russian thistle as when grown in pure culture, but when nonmycorrhizal, shoot biomass was about 30 percent less than that of the pure culture plants. While shoot biomass of Russian thistle remained greater than that of either grass regardless of culture type or mycorrhizal status, colonization by VAM fungi consistently reduced shoot biomass of the alien. Stomatal conductance was significantly increased in the grasses with the formation of mycorrhizae, by as much as 300 percent, in both pure and mixed cultures. In contrast, conductance in Russian thistle was significantly reduced with colonization by VAM fungi. The formation of mycorrhizae was clearly beneficial to the grasses, improving water relations and growth, and clearly detrimental to Russian thistle, which had reduced growth and water uptake. In the presence of VAM fungi, the competitive ability of mycorrhizal plants is enhanced whereas that of nonmycorrhizal plants is reduced so long as the plants are competing for the same limited soil resources (Reeves 1985).

VAM Fungi, Alien Weeds, and Rangeland Community Dynamics

Early seral nonmycorrhizal species, such as Russian thistle, are replaced by mycorrhizal species with the restoration of the inoculum potential of the soil (Biondini *et al.* 1985, Miller 1987). It is at this point in community development that cheatgrass, a facultative host, often becomes the dominant herbaceous species, and further successional change is inhibited.

The safe sites that allow native perennials to germinate and establish also provide cheatgrass

seed with favorable microsites (Evans and Young 1984), and cheatgrass seedlings usually outcompete the seedlings of native bunchgrasses (Piemeisel 1951, Harris and Goebel 1976, Thill *et al.* 1984). By virtue of its root phenology and rate of root growth, cheatgrass is able to exploit soil moisture much more effectively than native bunchgrasses (Harris 1967, 1977), thereby inhibiting the establishment of native perennial bunchgrasses and impeding successional change.

The relative competitive abilities of cheatgrass and native perennial grasses are probably not changed by mycorrhizal fungi, so long as both are colonized (e.g., Benjamin and Allen 1987). As networks of mycorrhizal hyphae are re-established, cheatgrass and any native perennials present are likely to be incorporated into these networks. Any benefit derived from the symbiosis would probably be enjoyed by both cheatgrass and the native grasses. The inhibition of successional change by cheatgrass suggests it retains its competitive advantage. In fact, cheatgrass may derive more benefit from the symbiosis than do the native grasses. In cereal crops, mycorrhizal colonization has given greater growth increases in winter-sown as compared to spring-sown grains (Buwalda *et al.* 1985). Dodd and Jefferies (1986, 1989) reported a high degree of root colonization by VAM fungi in autumn-sown crops by November or December, though environmental factors affected the persistence of the symbiosis. Later planting resulted in slower root growth during winter, and colonization generally declined with reduced rates of root extension. Since cheatgrass sustains root growth in lower, warmer soil horizons during winter, when native grasses are dormant, cheatgrass may benefit from mycorrhizal colonization from shortly after germination until senescence. The rapid rate of growth of cheatgrass would provide a strong sink for water and nutrients taken up by VAM fungi as well.

Additionally, the rate at which a plant's roots are colonized by VAM fungi can be influenced by the plant itself. Graham *et al.* (1991) compared the rates of mycorrhizal colonization of roots of woody species having low, intermediate, and high mycorrhizal dependencies. Species having a low mycorrhizal dependency were colonized less rapidly than were the other species, though the ultimate extent of colonization was the same. The authors noted that if a plant derived little benefit from mycorrhizal colonization and could also inhibit formation of the symbiosis, carbon that would otherwise flow to symbionts would be available for "needs that give a more immediate return on the investment [such as] production of new leaf area."

Cheatgrass is a facultative host, and its mycorrhizal dependence is lower than that of native perennials (Schwab and Loomis 1987). When grown in monoculture, the growth of cheatgrass was inhibited by VAM fungi (Schwab and Loomis 1987, Benjamin and Allen 1987). When grown in a mixture where bluebunch wheatgrass was most numerous, cheatgrass shoot biomass and phosphorus content was greater in mycorrhizal than nonmycorrhizal treatments, but in mixtures where cheatgrass was most abundant, VAM fungi inhibited shoot growth of cheatgrass and phosphorus content was lower (Schwab and Loomis 1987). Cheatgrass did not benefit from mycorrhizal colonization except when the relative density of mycorrhizal competitors was high. If cheatgrass is able to inhibit colonization of its roots by VAM fungi, carbon that would flow to symbionts could instead support vegetative growth. It may be that cheatgrass allocates its carbon to growth (i.e., space capture) during the period when the native perennials are dormant, and becomes a significant sink for soil resources taken up by VAM fungi only late in its development, when growth is most rapid. That is, cheatgrass may function as a sink for resources captured by mycorrhizae when doing so denies resources to the native perennials, and may otherwise minimize carbon allocated to mycorrhizal fungi.

Mycorrhizae and Seedling Establishment

It has been demonstrated that nutrient transfer via VAM mycelium from mature plants to seedlings occurs and is sufficient to increase seedling growth (Whittingham and Read 1982, Francis *et al.* 1986). One possible mechanism by which native perennial bunchgrasses could replace alien weeds would be the preferential flow of assimilates from mature plants to their progeny through the mycorrhizal network. Coevolved mutualists may exchange nutrients, water, and carbon more efficiently than would a profiteering alien, such as cheatgrass, and any measure of host specificity (McGonigle and Fitter 1990, Anderson 1988) could compound the effect. If this asymmetry of benefit were the case, the asymmetry of competition between seedlings and larger or mature plants would be reduced or

even eliminated. Mature plants could subsidize the growth of seedlings, increasing the probability of seedling survival (Grime *et al.* 1987). Once a long-lived perennial bunchgrass became established, the probability of successful establishment of additional individuals of that species could be enhanced.

Since seed density generally declines exponentially with increasing distance from the parent plant, it follows that seedling density should be greatest near the parent. If assimilates flowing from mature plants into the mycorrhizal network were taken up by nearest neighbors, a mature plant could, indirectly, increase the chances of successful establishment of its progeny. This type of seedling subsidization does not appear to necessarily be the case, however. Chiariello *et al.* (1982) found the movement of labeled phosphorus from donor plants to receivers could not be predicted on the basis of proximity, size, or taxon in a serpentine annual grassland. Patterns of translocation could be different in a perennial grassland featuring a mix of established plants and seedlings; growth form and phenology could also affect translocation patterns.

Assimilates do tend to move through the hyphal network from sources to sinks. Heavily shaded seedlings accumulated up to six times more labeled carbon than partially shaded seedlings (Francis and Read 1984). Thus, the transfer of assimilates may reduce asymmetrical competition and increase seedling survival. Eissenstat and Newman (1990) investigated mycorrhizal mediation of competition between seedlings and large plants. The investigators compared the growth of unshaded seedlings of buckhorn plantain (*Plantago lanceolata*), a forb, in soils with and without both VAM fungi and large plants of the same species. The presence of large plants stimulated colonization of seedlings by VAM fungi, and mycorrhizal seedlings obtained more nitrogen and achieved greater growth than nonmycorrhizal seedlings. However, both mycorrhizal and nonmycorrhizal large plants were equally effective in suppressing seedling growth. Though the mechanism was not demonstrated, the study suggests the intensity of competition between large plants and seedlings is not lessened by mycorrhizal fungi.

Contrasting results were obtained using a mixture of grasses and forbs, however (Grime *et al.* 1987). In this experiment, mycorrhizal and nonmycorrhizal *Festuca ovina* seedlings were transferred to flats and allowed to establish. Seeds of a mixture of grasses and forbs which commonly occur together were then added. Biomass of mycorrhizae-hosting (mycotrophic) seedlings was significantly greater in the mycorrhizal treatments, whereas biomass of the mycorrhizal canopy dominant, *F. ovina,* was significantly reduced. The biomass of nonhost (nonmycotrophic) plants was unchanged. Additionally, VAM allowed greater species diversity; seedlings which died in the treatments lacking mycorrhizae survived given VAM.

Future Research

Study of the role of mycorrhizal fungi in rangeland systems is needed. The growth response of rangeland grasses to colonization by VAM fungi depends upon the severity of environmental stress and intensity of interference, the plant species, the species of fungal symbionts, and their phenologies. Until this research is completed, little more than speculation is possible.

The mycorrhizal dependence of cheatgrass and especially the native perennial grasses needs to be determined. Patterns of variation in this dependence should be studied. Successional, seasonal, phenological, and density changes may all affect interactions among symbionts. Additionally, seasonal and successional changes in the composition and abundance of the community of VAM fungi in rangelands needs greater study. The rates of colonization of cheatgrass and native bunchgrass seedlings may provide insights into the timing of competitive interactions among these species and also their allocation patterns. Patterns of soil resource transfer via VAM mycelium in semiarid perennial grasslands need to be investigated. This could be accomplished by repeating the experiment of Chiariello *et al.* (1982) in suitable locations.

The relative competitive abilities of cheatgrass and native perennial grasses given mycorrhizal fungi, particularly over the long term, require study. There is a possibility of differential benefit among species (e.g., Allen and Allen 1986). Evolution of the ruderal strategy in plants is correlated with a reduction in mycorrhizal dependence (Trappe 1987). Fitter (1977) showed that velvetgrass derived more benefit from a mycorrhizal symbiont than did perennial ryegrass, despite the facts that both species hosted VAM fungi and the two species were equal competitors in the absence of mycorrhizae. Other experimental results have shown later emerging seedlings to derive greater benefit from the mycorrhizal symbiosis than did

already established plants (Grime *et al.* 1987). In stress-tolerant species, plasticity of the root system (the capacity to respond to and exploit transient nutrient-rich microsites) may be largely a function of the fungal symbiont.

Though benefit to mycorrhizal seedlings has been demonstrated (Whittingham and Read 1982, Francis *et al.* 1986), VAM mediated transfers from mature plants to juveniles under conditions of interspecific competition have received scant study. Repeating Eissenstat and Newman's (1990) experiment using a mature native bunchgrass and shaded and unshaded seedlings of both cheatgrass and the native would be one way to investigate the role of VAM fungi in rangelands. The microcosm approach of Grime *et al.* (1987) would be another excellent method of study. In sagebrush-grass communities, both shrub and grass seedlings are found primarily beneath the canopies of larger plants (Eckert *et al.* 1986, Miller 1987). In this situation, asymmetrical competition may be reduced as a result of assimilate transfer from sources to sinks.

Conclusions

Community dynamics in sagebrush-grass systems were radically altered with the introduction of domestic livestock and alien annuals and by fire suppression. Community composition through succession is now fundamentally different, with alien annuals comprising the early seral stages and inhibiting the re-establishment of native bunchgrasses. Mycorrhizal fungi appear to play an important role in succession in rangeland systems. Alien pioneer species are nonmycorrhizal and growth is inhibited in these species given colonization of their roots by VAM fungi. The establishment of native grass species is aided by mycorrhizal fungi, as VAM fungi increase the efficiency with which the soil volume is exploited by host plants and can inhibit nonmycorrhizal plants. Rangeland plants hosting VAM fungi generally have improved water relations, and water is the most limiting factor in the rangeland environment.

However, cheatgrass may derive more benefit from fungal symbionts than do native bunchgrasses. Cheatgrass grows rapidly, belowground in winter and aboveground in spring, providing a strong sink for nutrients, water, and carbon translocated via the hyphal network. Native perennial grasses become quiescent during the cold of winter; rapid growth by the natives is usually limited to spring. The competitive relationship described by Harris (1967), where cheatgrass was much more effective in sequestering soil moisture than was a native bunchgrass, is probably not altered by mycorrhizal fungi. Cheatgrass remains a highly effective competitor for soil moisture due to its phenology, rapid growth, and ability to host VAM fungi.

If, however, assimilates tend to flow from source to sink and to nearest neighbors, a mature plant could effectively subsidize the growth of its nearby seedlings. This could be an important mechanism for reoccupation of a site by native bunchgrasses. Assimilates may be more efficiently transferred among coevolved mutualists than to a facultative alien host. If assimilates are more efficiently transferred from a native bunchgrass to seedlings of native bunchgrasses, then VAM fungi have an important role to play in the restoration of Intermountain rangelands. Many questions remain unanswered, and additional research is needed. The roles of mycorrhizal fungi in seedling establishment and competitive interactions among the seedlings of native and alien grasses and among plants of different sizes are in need of study.

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Effects of Fluctuating Flows on the Population Dynamics of Rainbow Trout in the Spokane River of Idaho

Abstract

Rainbow trout (*Oncorhynchus mykiss*) were studied in 1985 and 1986 in the Spokane River, Idaho, to evaluate possible factors limiting abundance and survival. A mark and recapture estimate made in the fall 1985 was 19,029 fish and standing crop was estimated at 5.2 g/m² in a 7.9 km reach. Rainbow trout growth rates were above average for the region with fish averaging 140-155 mm in length by the end of the first year. Estimates of total instantaneous rate of mortality (Z) were 1.35 using catch curves and 1.13 to 1.44 based on tag returns. Exploitation corrected for nonresponse was 8.9 percent making instantaneous rates of fishing mortality (F) 0.16 and natural mortality (M) 1.19. Annual survival for recruited fish was less than 30 percent. Post spawning, over winter mortality, high zinc concentrations, high summer temperatures and/or low summer flows may have contributed to the high natural mortality. Spawning commenced in the Idaho reach about 1 April. Variable year-class strengths appeared to correlate with river flow between the spawning period (early spring) and establishment of feeding territories (1 July) during the first summer. Fry production was minimal in 1986. Sampling young-of-the-year trout in the fall and examination of the hydrograph could provide fishery managers with two years advance planning to supplement weak year-classes.

Introduction

The Spokane River, Idaho, has sustained a popular wild rainbow trout (*Oncorhynchus mykiss*) fishery for many years. Recently, however, fishermen have reported declines in the size and number of trout. Excessive harvest, lack of spawning habitat and dam operations have been suggested as possible causes (Idaho Department of Fish and Game 1985). Despite the introduction of brown trout (*Salmo trutta*) rainbow trout remain the principal game fish (Bennett and Underwood 1988). In Idaho, the Spokane River has been managed under a general six fish creel limit whereas downstream in Washington, restrictive terminal gear and creel limits have been imposed.

Some angler groups in Idaho have requested more restrictive regulations, such as lower creel limits and/or size limits. Additional data are needed on abundance, mortality, growth and recruitment. Our objectives were: 1) to investigate the population dynamics of rainbow trout in the Spokane River; and 2) to evaluate factors affecting rainbow trout survival and abundance.

Study Site

The Spokane River forms at Post Falls Dam (Figure 1), the outflow of Lake Coeur d'Alene (10,121 hectares, 648.6 m elevation). Lake Coeur d'Alene and the Post Falls Dam are separated by a long (14.5 km) shallow arm that restricts outflow to the lake's surface water. The river flows west from the lake, through the city of Spokane, Washington, and joins the Columbia River at Lake Roosevelt. At Post Falls Dam the river drains approximately 958,300 hectares including both highly developed and roadless areas.

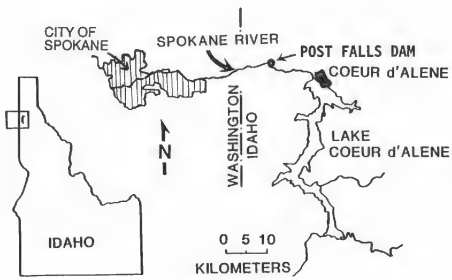

Figure 1. The Spokane River located at the outfall of Coeur d'Alene Lake, in northern Idaho and the study area from Post Falls Dam downstream to the Idaho-Washington border.

The study area was the 10 km reach between Posts Falls Dam and the Idaho-Washington border. The river in the study area is bordered by agricultural land and expanding residential developments. Mean river width was 58.8 m and mean high and low instantaneous flows were 623 m^3/s and 14 m^3/s. During spring runoff the lake fills and river flow is normally uncontrolled whereas during summer, flow equals lake intake (minus

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evaporation) and is augmented by lake storage for hydroelectric generation in late August or September. At low flow the river follows a riffle-pool-run sequence with a gradient of approximately 1.8 m/km. The channel is generally large cobble with bedrock exposed in scoured pools. Water temperatures during this study ranged from 2 to 24 C. River conductivity typically ranges from 50 to 80 umhos (Funk *et al.* 1975).

Methods

Fish collections were made in March, June, September, and October 1985 and June and October 1986 from drift boats equipped with boom-type electrofishing equipment. Each boat was equipped with two arrays of anodes and cathodes, a 3,500 or 2,900 watt generator, livecar, and was operated by a crew of two or three (one oarsman plus netters). Pulsed DC current was provided via a Coffelt VP-15 pulsator unit. Fish were usually captured and processed in the same riffle-pool segment of stream from which they were captured.

Fish were measured for fork length (nearest mm) and a subsample weighed to the nearest gram. Trout <170 mm were considered too small for tagging. Captured fish (>170 mm) were measured (fork length), tagged with serially numbered jaw tags and released. A stratified subsample (Ricker 1975) of up to 20 scale samples (n = 10 in 1986) per 25 mm length group was taken in the fall 1985 and 1986. Back-calculated length at annulus was determined by direct proportions, and corroborated by length-frequency distributions (Tesch 1978). Reward tags worth $5.00 were placed on 4 to 20% of the jaw tagged fish to estimate angler nonresponse (Henny and Burnham 1976).

Abundance estimates of Age-1+ and older fish (>130 mm) were made in the fall of 1985 using a modified Petersen mark and recapture estimate (Ricker 1975). Fish were marked using an adipose fin clip, released and recaptured 12 days later to allow for redistribution (Vincent 1983). Also, we jaw tagged 378 trout to assess movement to evaluate the assumption of a closed population. Catch efficiency curves were used to divide fish into size groups for more accurate population estimates (Vincent 1983). Average weights were calculated for the size groups and multiplied by the population estimates to estimate standing crop. Formulas for each estimator are listed in Table 1.

Total instantaneous rate of mortality and fishing and natural mortalities were estimated by catch curves (Everhart and Youngs 1981) and annual tag returns (Ricker 1975; Table 2). Trout were captured, tagged and released in March, June and September 1985 and June 1986. Tag return data was then available for two years from the March and June 1985 releases and one year from the September 1985 and June 1986 releases. Instantaneous fishing mortality (F) was calculated from annual exploitation (E) based on tag returns. Instantaneous natural mortality (M) was calculated as the difference between total and fishing mortality (Table 2).

The study area was stratified into upper, middle and lower sections and north and south banks to estimate the abundance of Age-0 fish along the river margin. We snorkeled randomly selected transects (35 per stratum each 10 m long and 2 m wide) once in July 1986 (Everhart and Youngs 1981; Schaeffer *et al.* 1986).

The relative strengths of the 1984, 1985 and 1986 year-classes were evaluated qualitatively by snorkeling the same reaches of river in July 1985 and 1986 and by comparing length frequency distributions from electrofishing data. Discharges from Post Falls Dam between 1 March and 30 June for 1984, 1985 and 1986 were examined to determine if any relationship existed between year-class strength and discharge during the spawning and incubation seasons.

Results

Abundance and Mortality

We estimated 19,029 (95% C.I. = 15,786 and 22,271) Age-1 and older rainbow trout (>130 mm) were present in the study area in the fall of 1985 based on 1,014 marked fish released and 111 recaptures of 1,950 fish examined for marks. The standing crop was estimated to be 5.2 g/m^2.

Estimates of total instantaneous rate of mortality from catch curves were 1.35 for pooled data (Figure 2), 1.27 and 2.10 for 1985 and 1986, respectively. Estimates of total instantaneous rate of mortality using single lots of tagged fish were 1.44 (March 1985 release) and 1.28 (June 1985 release) and the pooled estimate from releases in June 1985 and 1986 was 1.13.

Returns from fish tagged in March and June 1985, and June 1986 were similar whereas returns from those tagged in September 1985 were lower

TABLE 1. Formulas used for population estimates of rainbow trout in the Spokane River, Idaho.

Population estimate Age 1+ and older:

$$N = \frac{(M + 1) \cdot (C + 1)}{(R + 1)}$$

where,

N = estimated number of fish in the study area,
M = the number of fish marked,
C = the number of fish examined for marks,
R = number of recaptured marked fish.

$$V_{(N)} = \frac{N^2\left[\frac{(N - M) \cdot (N - C)}{M \cdot N \cdot (N - 1)}\right]}{}$$

where,

$V_{(N)}$ = the variance of the estimate population.

Population estimate Age-0 fish:

$$N = \frac{A}{a} \cdot \Sigma Ni$$

where,

A = the number of possible quadrats,
a = the number of quadrats sampled,
Ni = the number of fry observed in the ith quadrat.

$$V_{(N)} = \frac{A^2 - (aA)}{a} \cdot \frac{(a\ Ni^2 - (\Sigma Ni^2))}{a\ (a - 1)}$$

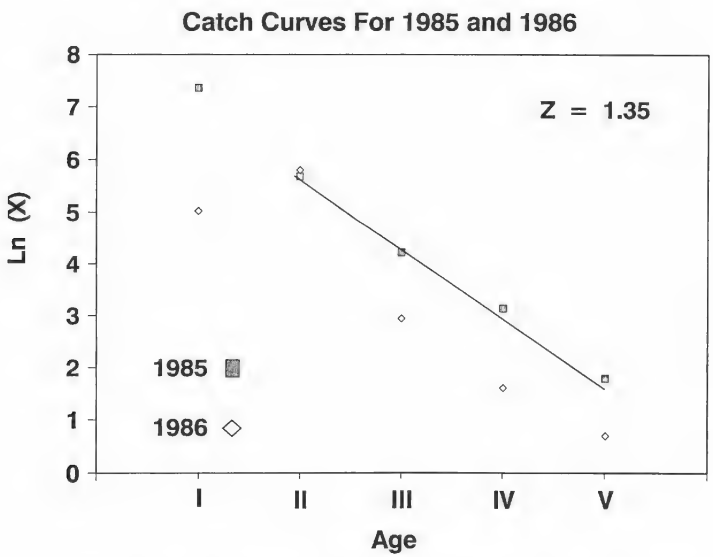

Figure 2. Plot of the natural logarithm of the electrofishing catch of rainbow trout from fall 1985 and 1986 collections, from the study area. The instantaneous rate of mortality (Z) is the slope (absolute value) of the regression line. The line represents mortality for the pooled data for 1985 and 1986.

TABLE 2. Formulas used to estimate survival and mortality statistics of the rainbow trout population in the Spokane River, Idaho.

Symbols:

A = total annual mortality
E = annual fishing mortality
F = instantaneous fishing mortality
M = instantaneous natural mortality
S = annual survival
Z = total instantaneous mortality
$V_{(s)}$ = variance of the estimate

Chapman-Robson estimate of survival:

$$S = T/n + T - 1$$

where,

S = the estimate of annual survival,
T = the sum of the coded age multiplied by their frequencies,
n = the sample size.

$$V_{(S)} = S[S - (T - 1)]/(n + T - 2)$$

Estimate of survival from tag returns (Ricker 1975):

$$S = R_2/R_1$$

where,

S = the estimate of annual survival,
R_1 = recaptures during the first year,
R_2 = recaptures during the second year.

$$V_{(s)} = [S(1 - S)]/R_1$$

and

$$S = R_{12}\,(M_2/M_1)R_{22}$$

where,

M_1 = number of fish marked the first year,
M_2 = number of fish marked the second year,
R_{12} = first year fish recaptured the second year,
R_{22} = second year fish recaptured the second year.

$$V_{(s)} = S^2\,(1/R_{12} + 1/R_{22} - 1/M_1 - 1/M_2)$$

than the releases in spring and summer (Table 3). Nonresponse was similar to that observed in other systems (Rieman 1987) based on the return of reward tags (mean = 42%). The mean annual exploitation rate weighted by the number of tagged fish was 9.2 percent (reward tags) or 8.9 percent (regular tags corrected for non-response). The highest estimate of instantaneous fishing mortality was 0.34 based on the pooled catch curve estimate of tagged fish which was equivalent to an exploitation rate of 18.8 percent, and this was the rate used to avoid overharvest and be consistent with a conservative management style. With the 18.8 percent

TABLE 3. Summary of Monel jaw tagged fish released in the Spokane River, Idaho.

		Regular tags		Reward tags	
Month	Year	Number released	Percent returned	Number released	Percent returned
March	1985	331	6.3%	32	9.4%
June	1985	303	6.3%	38	7.9%
Sept.	1985	362	2.2%	16	18.8%
June	1986	274	5.1%	70	7.1%

exploitation rate, the instantaneous natural mortality was 1.01, about 75 percent of the total annual mortality (Table 4).

TABLE 4. Summary of annual and instantaneous rates as related to levels of exploitation in the Spokane River, Idaho. Symbols used were: S = annual survival; A = annual mortality; E = annual exploitation; F = instantaneous fishing mortality; M = instantaneous natural mortality; and Z = total instantaneous mortality.

	Rates				
Method of estimation	S	A	F	M	Z
Catch curves (W/E = 0.092)					
1985	0.279	0.720	0.162	1.11	1.27
1986	0.122	0.877	0.218	1.87	2.09
Pooled	0.260	0.740	0.167	1.18	1.35
Chapman-Robson (W/E = 0.092)					
1985	0.253	0.747	0.168	1.20	1.37
1986	0.324	0.676	0.153	0.97	1.13
Pooled	0.216	0.784	0.179	1.35	1.53
Catch Curves (W/E = 0.188)					
1985			0.330	0.94	
1986			0.447	1.64	
Pooled			0.342	1.01	
Chapman-Robson (W/E = 0.188)					
1985			0.344	1.03	
1986			0.313	0.82	
Pooled			0.366	1.29	

[1]18.8% estimated from reward tags released in September 1985, 9.2% is the average return of reward tags weighted for the number released.

Age and Growth

Five age classes were present in the electrofishing catch. Growth rates were above average for rivers in this area (T. Bjornn, Idaho Cooperative Fish and Wildlife Research Unit, Personal Communication), with fish averaging 140-155 mm in length by the end of the first year (Table 5). The least-squares regression equation best describing the length (L) – Weight (W) relationship for 1985 was $Log_e(W) = -10.77 + 2.90Log_e(L)$; $Log_e(W) = -9.95 + 2.76Log_e(L)$ for 1986; ($r^2 = 0.97$ for both years).

Year-class Strength

The 1984 year-class was the most abundant cohort in all samples collected in 1985 and 1986 (Figure 3). Fish of the 1985 year-class were collected in June 1986 far less abundantly than the 1984 year-class at the same age. Underwater observations indicated that fry densities of the 1986 year-class were lower than those of the 1985

TABLE 5. Back-calculated fork length (mm) at annulus for rainbow trout captured by electrofishing in the Spokane River, Idaho, in September 1985 and October 1986.

		Age				
1985	n	1	2	3	4	5
	72	153				
	70	153	244			
	28	148	242	305		
	15	164	257	311	355	
	4	166	227	307	354	396
Average		154	245	307	354	396
1986	19	134				
	45	140	218			
	18	140	232	305		
	2	157	227	319	371	
Average		139	222	306	371	

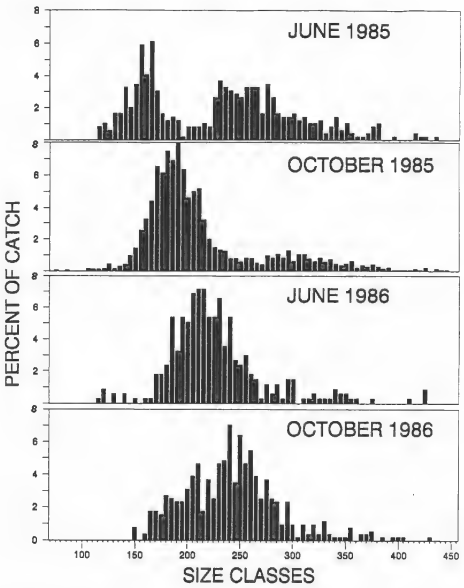

Figure 3. Length-frequency distributions of rainbow trout collected in June and October 1985 and 1986.

year-class. Areas that supported fry in 1985 did not contain fry in 1986. In 1986, 37 fry were observed in 22 of 210 quadrats (12%) out of 1694 possible quadrats. An estimate of 315 Age-0 fish (95% C.I. $158 \leq N \leq 471$) was calculated for the study area in June 1986. Length-frequency data for October 1985 and 1986 corroborated our snorkel data that young-of-the-year were present in the electrofishing sample in October 1985, but not in October 1986 (Figure 3).

Discussion

We estimated over 1,900 fish/km in the Idaho section of the Spokane River, a larger rainbow trout population than an earlier estimate of less than 425 fish/km (Bailey and Saltes 1982). The fall biomass of 5.2 g/m² (rainbow trout >130 mm) was similar to that of a self-sustaining rainbow trout population in Virginia (3.13 to 4.30 g/m², Neves *et al.* 1985), for a tailwater fishery in the Green River of Wyoming (4.96 g/m², Wiley and Dufek 1980), and a combined population biomass of brown and rainbow trout (>198 mm) in the Madison River of Montana (5.9 g/m², Vincent 1969). Standing crops for Age-0 and Age-1 fish were estimated as high as 10.4 and 16.0 g/m² in a productive rainbow-steelhead stream in eastern Idaho (Bjornn 1978). In other studies on trout summarized by Lorz (1975), estimated standing crops ranged between 0.2 and 22.4 g/m².

Growth rates of rainbow trout in the study area were good. Annual growth increments during the first year were similar to other populations in the same latitude (Wydoski and Whitney 1979).

Annual mortality in the lower Spokane River was 74 percent per year. Estimates of total mortality (Z) from catch curves and tag returns were similar and exploitation estimates were similar to those previously reported (4-9%) for the river (Bailey and Saltes 1982). In comparison, instantaneous rates of mortality ($Z = 1.35$; $F = 0.34$; $M = 1.01$) for rainbow trout in the Spokane River were slightly higher, but in the same proportions as those reported by Wiley and Dufek (1980) for rainbow trout in the Green River ($Z = 1.12$; $F = 0.20$; $M = 0.92$). Petrosky and Bjornn (1988) reported total instantaneous mortality rates of 1.93-2.06 for yearlings and older rainbow trout over a three year period for Big Springs Creek, Idaho, a productive stream in eastern Idaho. Based on these studies, we do not believe the mortality of rainbow trout in the Spokane River in Idaho is uncommonly high. Populations in other streams that produce quality fisheries exhibit even higher mortality rates. The low fishing mortality was a surprise. Although fishing effort was not quantified, the close proximity of the cities of Coeur d'Alene and Spokane led us to expect higher fishing mortality. Natural mortality composed a major proportion of total annual mortality since mortality due to fishing was low (<20%). Nonetheless, perceived declines in the Spokane River fishery are difficult to assess with the limited historical data base. The decline in fishing quality could be the difference between even lower fishing mortality years ago and the present rate.

Recruitment during 1986 was lower than expected. The estimate of Age-0 rainbow trout in the 10 km study area was only 315 fish. Based on our mortality calculations (Figure 2), we estimate there should have been about 10,000 Age-0 fish to produce the abundance of older fish observed in 1985 and 1986. The low number of Age-0 fish suggests that recruitment of young-of-the-year fish was poor in 1986 despite the moderate standing crop of older fish. The low number of Age-0 fish observed in 1986 is one indication that recruitment can be more variable among years, although examination of the catch curves (Figure 2) for Ages 2-5 rainbow trout suggests that recruitment was reasonably stable in the early 1980s.

Size and age structures of the rainbow trout population in the Spokane River were strongly correlated with growth and mortality. Growth and fishing mortality are similar to other quality trout fisheries, but natural mortality reduces the population up to 64 percent annually allowing few fish to reach large size (older age classes). A combination of high natural mortality and low recruitment can shift the structure of the population (Figure 3). Substantial year-class variations occur in the Idaho section of the Spokane River under conditions of high natural mortality and variable recruitment.

The source of natural mortality in the Spokane River is unknown. Possible causes include: overwinter mortality (Shetter 1967) as indicated by the low return of fish tagged September 1985 (Table 3); high zinc concentration (0.12-0.62 mg/l, Funk *et al.* 1975); post-spawning mortality (Ferguson and Rice 1980); high (24 C) summer water temperatures (Kaya 1978; Hokanson *et al.* 1977); and water level fluctuations (Mundie 1969; Holden 1979). It is unlikely that natural mortality could

be easily reduced and therefore, the quality of the fishery depends upon recruitment and spawning success. Strong year-classes are necessary to maintain abundance and provide enough fish to survive to trophy size.

Factors affecting recruitment seem to occur between spawning (around 1 April; Figure 4) and some time shortly after emergence (15-25 June). The estimate of young-of-the-year rainbow trout was conducted in July 1986 and year-class strength was established prior to our sampling. The 1984 year-class, first sampled as Age-1 fish in 1985, remained strong throughout the study (Figure 3).

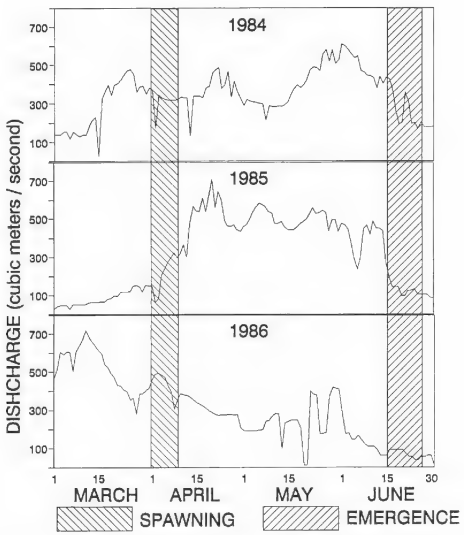

Figure 4. Minimum daily discharges (m^3/sec) in the Spokane River from Post Falls Dam from 1 March through 30 June 1984, 1985 and 1986. Spawning and emergence times of rainbow trout are also shown.

Year-class strength for 1984, 1985 and 1986 was variable and correlated with their respective spring hydrographs (Figure 4). The strong 1984 year-class was associated with high, relatively constant flows between 1 April and 25 June. Spring runoff continued into late June and minimum daily discharge fluctuated less during embryo incubation in 1984 than in 1985 and 1986. The 1985 year-class, intermediate in abundance, occurred with intermediate flows during spawning, but serious reductions in flows occurred near emergence time. The weak 1986 year-class developed in a year of fluctuating, low flows. Spring runoff subsided late in May 1986 and flows fluctuated greatly especially in May when alevins were most vulnerable. Nonetheless, the link between water levels and recruitment is still unclear in this section of the Spokane River. However, our cursory observations indicate that spawning gravels are only inundated above flows of 200-300 m^3/sec. Flow fluctuations cause mortality to embryos and alevin through reduced oxygen levels, stranding and desiccation (Fraser 1972; Reiser 1981; Neitzel and Becker 1985). Becker *et al.* (1983) found that dewatering became more critical as embryo development progressed and especially between hatching and emergence.

We found that quadrat sampling is a technique to assess year-class strength in the Spokane River and other rivers that experience similar fluctuation in flows. Snorkel transects should be conducted shortly after emergence to assess the relative strength of the year-class. Cursory predictions of year-class strength from the examination of the hydrograph and an index based on transect sampling of young-of-the-year could provide enough information for a manager to anticipate stocking or other corrective management action to stabilize recruitment and ultimately, the fishery. Similar information on year-class strength has been used to predict catch rates (Engstrom-Heg 1986). Since rainbow trout in the Idaho section of the Spokane River generally are not available to the fishery until their third summer, such a strategy would allow up to two years lead time for implementation of the appropriate management action (i.e., stocking, season closure, etc.).

In summary, we suggest that the quality of the fishery in the Idaho section of the Spokane River will fluctuate depending on climatic conditions and spawning success. Strong year-classes are necessary to offset the high natural mortality to produce a quality fishery and will probably only occur with high, relatively constant flows between April and late June.

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Book Review

Walks of the Pacific Northwest.

Gary Ferguson. Prentice Hall Press. $14.95.

With his book, *Walks of the Pacific Northwest,* Gary Ferguson succeeds admirably in a difficult assignment. The task of choosing 75 day-hikes from the myriad of destinations in Oregon, Idaho, and Washington is not an easy one. Neither is the job of describing the uniqueness of each walk—including that area's ecology, history, and geology—with well-chosen and vivid prose.

Despite the difficulty of selecting both appropriate trails and appropriate words, Ferguson did a marvelous job as a walker and as a writer.

The book's 270 pages are filled with adequate maps that roughly plot the destinations and dozens of pleasing line drawings of flora and fauna found along the pathways. Each of the 75 selected walks receives several pages of step-by-step narrative describing sights along the trail, as well as a listing of total trail miles and specific how-to-get-there information.

Ferguson divides the Northwest into four ecological zones: the forest, the coast, the mountains and the desert, and lists approximately the same number of hikes for each zone. Too many guidebooks shun the rough beauty of the desert, and Ferguson is to be commended for remembering that much of the Northwest is not postcard-perfect trees and meadowland.

Within each of those four zones, the book is further divided by state (Oregon, Washington, Idaho), resulting in a text with a total of twelve sections. Because of that structure, it is easy for readers to locate a walk near their route.

The 75 walks are just that—walks, not hikes, on trails of less than a mile to a half-dozen miles in length. They are not isolated trails with few human visitors, but are relatively well-known and well-travelled routes. That is a drawback for those who prefer their solitary sojourns, but for the average guidebook buyer who chooses driving over walking virtually all the time, the selections are good ones.

Within the narrative Ferguson provides for each walk, the emphasis is on information, not on empty or over-wrought descriptions. The book is full of great tidbits of information that would help anyone who walks with their eyes open to see even more, and to enjoy the trail even more.

Ferguson treats his readers on almost every page with a delightful morsel. For example, on page 60 and 61, he rambles on enjoyably about the usefulness of downed trees for all the forest's creatures. He introduces the term "nurse logs" in reference to a giant log along the trail and the tiny trees and plant community thriving on its surface. His explanation of the complex interaction within the forest that is visible along that walk is an excellent lesson in applied ecology.

A few pages earlier, Ferguson devotes a paragraph to a woodland cabin adjacent to another trail. The historical footnoting is so complete that readers are told not only about the cabin's builders, but also that the builders' diary—now in storage at Washington State University—notes their fine view (a vista now shrouded completely by the last half-century's forest growth).

On different pages along the way, readers are told how barnacles attach to rocks, how pikas survive the winter, and about the traditional uses for mullein—among thousands of other not necessarily vital bits of history, geology, natural history, and Native American lore.

All that informing is not mixed in a dry and boring fashion. Ferguson knows the way to polish a phrase to a most appealing shine. Try this sentence, about an out-of-the-way destination: "The Settlers Grove of Ancient Cedars does not just show up as some kind of unexpected gift from the highway gods as you fly down the exit ramp looking for a bathroom." Here's another, a gem about Idaho's greatest undammed river: "To lovers of wild rivers, the various forks of the Salmon are a kind of Xanadu—a fantasy place so magnificent, so completely freeflying that you almost hold your breath for fear they will dissolve before your eyes."

In sum, those who treasure the Northwest in all its fantastic diversity, and who prefer comfortable day-hikes over backpacking into the bush, should try Gary Ferguson's great guidebook.

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